5-2017

Spatial Ecology of Coyotes and Cougars: Understanding the Influence of Multiple Prey on the Spatial Interactions of Two Predators

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SPATIAL ECOLOGY OF COYOTES AND COUGARS: UNDERSTANDING THE INFLUENCE OF MULTIPLE PREY ON THE SPATIAL INTERACTIONS OF TWO PREDATORS

by

Peter J. Mahoney

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

2017

ABSTRACT

Spatial Ecology of Coyotes and Cougars: Understanding the Influence of Multiple Prey on the Spatial Interactions of Two Predators

by

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The extent to which predators regulate prey populations remains a subject of debate. Yet, when predator control is employed as a management strategy, it is often assumed that predators can and do regulate prey populations. From 2011 through 2015, I monitored the demography and space use of coyotes (*Canis latrans*) and cougars (*Puma concolor*) on Monroe Mountain in Fishlake National Forest, Utah as part of a larger collaboration investigating the impacts of coyote aerial control on mule deer (*Odocoileus hemionus*) neonate survival. My primary objective was to assess the impacts of anthropogenic regulation on the respective populations and identify any cascading effects relevant to mule deer management. To meet this objective, I established a monitoring program for both predators by deploying radio-telemetry collars (VHF and GPS) on each, documented predation events, established surveys for small mammals and lagomorphs to monitor primary prey populations during deer parturition (June – August), and collected data on the location and demographic composition of winter-removed coyotes. I analyzed

these data primarily in a community-based, animal movement and resource selection framework permitting the integration of data from multiple sources. When evaluating coyote aerial removal as a management strategy, I identified a spatial dependency in the ability to match removals with indices of deer recruitment as Wildlife Services Operations personnel were primarily limited by terrain and tree cover. Thus, matching treatment with deer fawning was highly variable with only a small number of sites where removals were effective. In addition, I found that coyotes selected for sites with the highest densities of lagomorphs while avoiding areas with a high probability of encountering cougars. Coyotes did not select for mule deer fawning sites, although individual coyotes that occupied resource-poor home ranges were more likely to do so. Cougars strongly selected for mule deer high use areas throughout much of the year, only switching to elk (*Cervus elaphus*) during the cougar harvest season (i.e., winter). Data from cougar kill site investigations match the observed patterns in cougar space use. My results suggest that predator-prey processes are multi-dimensional and dynamic through time, which likely contribute to the lack of resolution regarding the efficacy of predator control and the regulatory potential of predators in general.

(252 pages)

PUBLIC ABSTRACT

Spatial Ecology of Coyotes and Cougars: Understanding the Influence of Multiple Prey on the Spatial Interactions of Two Predators

Peter J. Mahoney

The coyote (*Canis latrans*) has expanded throughout much of North America over the past century following the regional extirpation of apex predators. These highly adaptable canids can occupy a variety of landscapes from the rainforests of Central America to the dense, human-dominated urban centers of the United States. As a generalist predator, coyotes can capitalize on a variety of food resources, including anthropogenic subsidies such as domestic livestock and food tailings at landfills. These tendencies often bring coyotes in direct conflict with humans, forcing managers to consider mitigation strategies ranging from the targeted removal of problem individuals to a broader reduction in population abundance. However, managing these wild canids is not without controversy. Thus, I take a science-based approach to understanding the nuances of coyote impacts on mule deer (*Odocoileus hemionus*). I present my findings from a 4-year study in southcentral Utah pertaining to the general ecology of coyotes and their primary competitor, the cougar (*Puma concolor*), as well as specific findings with regards to the efficacy of a predator control program used in mule deer management. My findings indicate coyotes generally favor areas with high lagomorph density over that of areas occupied by pregnant mule deer, suggesting deer fawn predation by coyotes may be opportunistic. Interestingly, coyotes strongly avoid areas utilized by cougars, which may

indicate cougars can regulate coyote access to deer. Cougars, on the other hand, strongly select for areas utilized by mule deer, which make up almost two thirds of their diet. However, during the cougar harvest season and over the winter months, cougars appear to be more willing to consume elk (*Cervus elaphus*), likely because of increased access and spatial overlap with elk. Finally, my evaluation of aerial control of coyotes as a management strategy for deer indicates that outcomes are often highly variable across space and among individual coyotes removed. However, there is some indication control can be effective at local scales where there is strong overlap between coyote removal and areas favored by pregnant deer. My results suggest that predator-prey processes are multi-dimensional and dynamic through time, which likely contribute to the lack of resolution with regard to the efficacy of predator control and the regulatory potential of predators in general.

ACKNOWLEDGMENTS

I thank Dr. Julie Young whose wisdom and guidance were everything I could have asked for from a major advisor. Thank you for the opportunity to conclude my graduate studies in an environment that was both amiable and ambitious, supportive and studious. I am very cognizant of my good fortune to have been a part of your lab, and am proud to have you as a friend and colleague.

I would like to thank the Utah Division of Wildlife Resources, USDA-WS National Wildlife Research Center, Utah State University, and the Ecology Center for their financial support of my field research and studies while a PhD student. I thank my committee composed of Drs. Eric Gese, David Koons, Jim Powell, and John Shivik for their guidance regarding life as a professional scientist and assistance with drafting my dissertation. Further, I would like to thank them for the patience they displayed throughout, but most especially during the final push toward my defense.

I would also like to thank Vance Mumford and Kent Hersey with Utah Division of Wildlife Resources and Kreig Rasmussen with the U.S. Forest Service for their year-round field and logistical support on Monroe Mountain. Their expertise and local knowledge benefited my safety, and that of my technicians, while working in the field, and contributed immeasurably to the quality of my dissertation. I thank Kevin Dustin and Mike Linnell with USDA Wildlife Services for their logistical support and expert advice regarding predators borne from years of field work.

I thank all my technicians, which included Isaac Kelsey, Matt King, Jeff Brown, Jared Moore, Carrie Jamieson, Patrick Schirf, Erin Wampole, Cliff Maehr, Zach Dustin,

Ryan Dillingham, and Nickoli Kallman, for many weeks or months of participation that was essential to the success of the project, all while tirelessly contending with my often stochastic and frenetic leadership in the field.

I thank my friends and colleagues in the Animal 'Predator' Ecology Lab, including Michel Kohl, Danny Kinka, Beth Orning, Julie Golla, Jarod Raithel, Aimee Tallian, Lacy Smith, Gavin Cotterill, Joel Ruprecht, Patrick Meyers, Brad Nichols, Pat Jackson, Ryan Kindermann, Sharon Poessel, Bryan Kluever, and many more, for their advice, support, and friendship.

I thank David Stoner for always lending an open ear, whether it be to discuss specifics with regards to predator-prey systems or how best to strike balance between life as an academic and as a father and husband. And to Clint Mecham, a friend and colleague whose expertise navigating the Utah's backcountry or with mountain lions I could not have done without, I thank you. I thank John Benson and Michel Kohl for endless willingness to provide a sounding board for all things professional or otherwise. Through your friendship, I have become a better scientist.

And foremost, I would like to express my deep gratitude to my family for bearing with me over the course of my seemingly never-ending life as a student. Your emotional, social, and financial support have been critical to my success and will not be forgotten. To my mother Diane and father Kevin, thank you for supporting my dream of pursuing the sciences, and for encouraging my curiosity in the natural world. Know that I recognize how difficult this must have been from our home in suburban Chicago, but you made it possible. To my brother Matt and sister Katie, for your tireless encouragement and support, as well as your active roles as Godparents, as well as uncle and aunt, to my

kids. And to Don and Louann, as well as Jake and Kaitlyn Trew, for supporting my family in so many ways, not the least of which was insuring all sorts of summer adventures for my children and wife during the long summers I was away in the field.

A special thank you to my daughter Gwynn, whose childhood has been shaped by the thrill of adventure in the field, juxtaposed with the struggles of my frequent and prolonged absences. You had the least say in the matter, but rose to the occasion again and again, especially as a friend and helper to your mother and little brother Ronan.

And to my wife, my life partner, for digging deeply into reserves of unprecedented patience long past their expiration date. Know that I recognize this accomplishment is just as much yours as it is mine. You are my world and my soul.

Peter J. Mahoney

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CHAPTER 1

INTRODUCTION

Carnivores play a fundamental role in maintaining biodiversity in ecological communities worldwide (Ripple et al. 2014). Intuitively, carnivores express their role most efficiently through the consumption of prey. While easily viewed through a one-dimensional lens, as we advance our understanding of predator-prey processes, we have become increasingly aware of the perturbations that travel throughout communities as a consequence of the dynamic interactions between predators and their prey (*e.g.,* Ritchie and Johnson 2009). Carnivores can induce numerical declines in prey and alter prey behavior (Sergio et al. 2008), which can in turn alter the spatial heterogeneity of landscapes or stochastic trends in prey populations with observable effects across the web of interconnected species within communities (Palomares and Caro 1999, Berger et al. 2008). Thus, carnivores can indirectly alter the consumptive and/or competitive processes at lower trophic levels, which in turn can influence the stability and diversity within communities (Estes et al. 2011).

The large spatial requirements, susceptibility to habitat loss and fragmentation, and slower reproductive life-histories of large carnivores have contributed to large-scale declines in predator populations (Cardillo et al. 2005), with potentially destabilizing consequences for ecological communities and ecosystem function as a whole (Estes et al. 2011). Conservation of large carnivores is further exacerbated by concurrent declines in native prey populations, inducing higher rates of livestock depredation and elevating the level of conflict with humans (Ripple et al. 2014). As a result, carnivores are increasingly subjected to anthropogenic population control measures in an effort to mitigate conflict

with humans over livestock or wild game. Yet, the charismatic disposition of many large carnivores has drawn the attention of conservationists and thus often serve as standard-bearers of many conservation movements worldwide (Sergio et al. 2008).

The conservation and management of large carnivores is a polarizing issue generating divergent opinions among diverse human communities, often along ideological, political, or geographical boundaries. However, nowhere is this rift in opinion greatest than along the urban-rural divide. Carnivore conservation can be quite controversial even within rural communities, particularly with greater recognition for the services they can provide to agricultural communities (*e.g.*, Ranglack et al. 2015). As large carnivore populations recover in areas where previously extirpated, or in scenarios where populations are in decline as a consequence of anthropogenic landscape use, we will need to consider management as a means of promoting coexistence in an increasingly human-impacted world (Woodroffe et al. 2005). This will not only require scientifically sound strategies for mitigating conflict, but also a significant public awareness and education campaign (Dickman 2010). Otherwise, efforts to promote coexistence may be in vain (Madden 2004).

One of the greatest challenges conservationists face is how to promote tolerance of animals that often present very specific challenges with measurable economic costs or safety concerns, particularly at local scales. Critics of carnivore conservation often emphasize 'conflict' as the primary motivation for predator control or event extirpation in more extreme circumstances. Yet, carnivore conflict can be quite nuanced, often involving some degree of domestic livestock depredation or damage (including the killing of domestic pets), competition over wild game, and in some instances threats to

human safety (Thirgood et al. 2005). While there is likely an added element of human psychology at play, particularly for those who neither suffer the economic consequences of living with predators or are at risk of encountering them (Thirgood et al. 2005), direct conflict is the most substantive argument for predator control with perhaps the greatest potential for mitigation.

The empirical support for top-down pressuring (i.e., regulatory control of prey by predators) within many terrestrial systems lends credence to the idea that regulating carnivores may positively affect prey populations. Assuming this holds true within specific systems, we then need to ask ourselves whether the methods used to regulate carnivores are both appropriate and effective given the ecology (or biology) of the carnivore in question, as well as whether the effects of removing carnivores manifest at scales relevant to our objectives (both temporally and spatially). In addition, we should recognize that predator control may have consequences beyond the objectives of management, particularly as it relates ecosystem function (i.e., community composition, nutrient cycling, and forage quality).

Generally, carnivore conflict mitigation can be partitioned into three broad methodologies: lethal removal, behavioral modification through non-lethal means, and financial compensation for damages. The type of conflict management employed, as well as the efficacy of said strategy, is often tremendously context-dependent and a reflection of the type of conflict, logistical constraints operating within a given system, and local economics (Treves and Karanth 2003). In addition, local attitudes towards conflict mitigation are likely as diverse as the people themselves and in some cases may take precedence over rigorous measures of efficacy in conflict management strategy (Dickman

2010). Although stakeholder input is invaluable towards finding resolutions with regards to wildlife conflict, any suggested mitigation strategy should be based on sound scientific principles and undergo rigorous investigation of the constraints on success, particularly given the financial costs and ethical positions associated with predator control efforts.

For the focus of my dissertation research, I worked in collaboration with the Utah Division of Wildlife Resources, USDA Wildlife Services, USDA-WS National Wildlife Research Center, and Brigham Young University to investigate the impact of a predator control program on mule deer (*Odocoileus hemionus*) neonate survival and population growth. Specifically, my work focuses on the lethal removal of coyotes (*Canis latrans*) and cougar (*Puma concolor*) harvest as it relates to wild game management. Although the research I present here will largely emphasize the carnivore perspective, I would like to acknowledge that these efforts were funded with an interest in developing a scientific understanding of predator-deer conflict in Utah and the broader western U.S., as well as strategies used to mitigate conflict with coyotes in particular. To successfully do so necessitates a keen awareness of the direct consequences of predation for mule deer populations. Although I provide only limited discussion on deer demography, this question will largely be addressed by our collaborators at Brigham Young University.

The common theme throughout my dissertation will be the importance of spatial context as it relates to predator-prey processes in general, while emphasizing the relevance of predator control strategies in mule deer management specifically. I make the overarching point that predator-prey processes are rarely one dimensional and that to understand the outcome of predator control programs, whether the affirmation or nullification of an impact, necessitates a broad, community-wide perspective on spatial

interactions and competitive processes for all key species within the system. Moving forward, it will be necessary to account for stochastic trends in populations, as well as climate, to better understand the nature of dynamic interaction strengths within predator-prey systems, particularly if we are interested in decoupling the effects of predators on their prey.

In chapter 1, I highlight the importance of spatial scale when evaluating the efficacy of predator control programs. All too often we rely on raw metrics of removal effort as predictors of control program success. Yet, this assumes space within our sampling units is homogenous with regards to control efficacy and impact. However, I demonstrate the substantial amount of heterogeneity present in a single system and that should be expected in most cases where large scale predator control programs are implemented. Further, I highlight the tremendous amount of variation in estimated impact of individual predators as a consequence of the location where they were removed and based on our understanding of movement within these populations. Together, these results demonstrate the need to explicitly account for space when quantifying the potential impact of predator removals.

In chapter 2, I emphasize the ecological context of the coyote-deer conflict by evaluating resource selection in coyotes, while explicitly accounting for primary prey availability, space use by parturient deer, carrion subsidies provided in the form of cougar kills, and spatial risk associated with cougar space use and distance to roads (*i.e.*, anthropogenic risk). I demonstrate that competitor interference and spatial partitioning with cougars is likely limiting the impact coyotes have on deer. Specifically, coyotes strongly avoided areas utilized by cougars, whose space use in turn coincided with

estimates of deer space use. And thus, coyotes did not select for (or avoid) areas utilized by deer. However, when evaluated on an individual level, coyotes that occupied resource poor home ranges (*e.g.,* low lagomorph densities) were more likely to select for areas utilized by parturient deer.

In chapter 3, I evaluated movement and space use in a harvested cougar population while accounting for the dynamic movements of their prey, mule deer and elk (*Cervus elaphus nelsoni*). I demonstrate that harvest may push cougars into more rugged terrain during the harvest season. This pattern appeared to coincide with a switch from selecting for areas used by deer outside the harvest season to selecting for areas utilized by elk during the harvest season. In addition, cougar kill data also indicated a slight shift in prey selection towards elk, with potential implications for overwintering deer demography.

In chapter 4, I outline a new method to classifying site fidelity patterns and associated behaviors from animal relocation data. The method I implement in this chapter was used to identify risky areas for deer and elk as it relates to cougar predation and to confirm the presence of fawns for some deer during the window for neonate parturition in chapter 2.

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CHAPTER 2

QUANTIFYING THE IMPORTANCE OF SPATIAL CONTEXT IN LARGE SCALE MANAGEMENT ACTION[1]

Summary

1. Predator control is often implemented with the intent of disrupting top-down regulation in sensitive prey populations. However, ambiguity around the efficacy of predator management, as well as the strength of top-down effects of predators in general, is often exacerbated by spatially implicit analytical approaches used in assessing data with explicit spatial structure. We highlight the importance of considering space in the case of a predator management study in southcentral Utah.
2. We analyzed data from a predator control study to assess the spatial match between coyote (*Canis latrans*) aerial removal risk and mule deer (*Odocoileus hemionus*) resource selection during parturition using a spatially explicit, multi-level Bayesian model. With output from this model, we were able to evaluate spatial congruence between management action (*i.e.*, coyote removal) and objective (*i.e.*, parturient deer site selection) at two scales: management area and home range of individual removed coyotes.
3. Our results indicated strong spatial heterogeneity in expected congruence between removal risk and deer site selection across large areas, and reflects logistical

[1] Mahoney, P.J., D. Stoner, R. Larsen, B. McMillan, K. Hersey, and J.K. Young. *Journal of Applied Ecology*.

constraints acting on the management strategy and differences in space use between the two species.

4. Synthesis and applications: We demonstrate that the outcome of individual predator removals were often spatially distinct from parturient deer resource selection; thus, emphasizing the need to weight individual removals when evaluating the impact of predator control programs. Although our approach is in the context of predator control, the methods are readily generalizable to any evaluation of management strategy where spatial context is an important driver of management success.

Introduction

Under the guiding tenants of the North American Model of Wildlife Conservation (Organ *et al.* 2012), the lethal removal of problematic species is permissible for 'legitimate purposes' following humane and scientifically sound strategies. Lethal predator control programs have been implemented to mitigate declines in threatened and endangered species (Harding, Doak & Albertson 2001; Smith *et al.* 2010) and to benefit economically valuable prey species throughout the USA, such as wild ungulates (Hurley *et al.* 2011; Kilgo *et al.* 2014) and livestock (Graham, Beckerman & Thirgood 2005; Berger 2006; Mabille *et al.* 2015). In both cases, management is often conducted on the basis of assumed impacts of predation rather than from a mechanistic understanding of the interactions between predators and managed prey populations (Ballard *et al.* 2001; Harding, Doak & Albertson 2001; Brown & Conover 2011). Indeed, few studies have critically assessed predator control and those that have done so lack consistency in

conclusions concerning management outcomes (Salo *et al.* 2010; Hurley *et al.* 2011; Bradley *et al.* 2015).

Although fundamentally a reflection of our inability to make broad generalizations about the regulatory potential of predators, the absence of consensus with regards to predator control is a manifestation of inconsistencies across studies, including differences in species' life history, control strategy, scale of inference, and analytical methods (Graham, Beckerman & Thirgood 2005). Many studies are limited to correlating raw removal effort (*e.g.,* absolute numbers of individual predators removed) with some metric capturing the desired management outcome (*e.g.*, survival or population growth). Yet in doing so, researchers often omit relevant confounding factors that potentially mask or exaggerate the impact of predator control on management objectives. Such factors are often independent of predator control strategy and can include influential environmental variables, such as climatic state or phenology (Durant *et al.* 2007; Griffin *et al.* 2011), that drive numerical responses in predator and prey populations or affect prey vulnerability (Hebblewhite 2005). Resource availability, defined broadly, can alter community composition (Tilman 1981), triggering additive or compensatory processes associated with species interactions within (Serrouya *et al.* 2015; Leo, Reading & Letnic 2015) and across trophic levels (Griffin *et al.* 2011). For example, the availability of alternative prey, including anthropogenic subsidies such as livestock and food waste, can contribute to variable impacts on managed prey populations (Knowlton, Gese & Jaeger 1999; Hurley *et al.* 2011).

Importantly, the individuals being removed as a result of control efforts are unlikely to have consistent impacts on prey populations (Jaeger *et al.* 2001; Blejwas *et al.*

2002). Individual behavioral differences attributable to experience, social status, and social learning are likely to be important predictors of individual impact and the success of a given control program (Mitchell, Jaeger & Barrett 2004). Variation in spatial proximity to the desired objective (*e.g.,* wintering yards, fawning sites, etc.) and proximity to management boundaries where recruitment of new individuals may be more frequent (Lieury *et al.* 2015) are also likely to influence an individual's effect on management goals. Similarly, the size of a management area relative to the movement characteristics of the focal species can directly affect detection, risk, and rate of recovery following removals (Stoddart, Knowlton & Taylor 1989). Although individual variation in behavior is difficult to quantify, defining the spatial context of individual removals is frequently possible, yet rarely accounted for in these assessments (Conner, Ebinger & Knowlton 2008).

Coyotes (*Canis latrans*) are often the focus of predator control efforts throughout much of North America, as a consequence of extensive range expansion over the last century and associated increases in conflict with humans over domestic livestock and wild game (Berger, Gese & Berger 2008; Magle *et al.* 2014). A common method used to mitigate conflict with coyotes in the western US is aerial gunning (hereafter removal) from fixed-winged aircraft or helicopters (Brown & Conover 2011). The desired outcome of this strategy is the targeted removal of problem animals or broad reduction in predator abundance, followed by a decline in predator-induced additive mortality in prey populations (Wagner 1997).

Coyotes can be effective predators of neonatal fawns (Freeman 2014; Kilgo *et al.* 2014; Seidler, Gese & Conner 2014). In many areas of the western United States, aerial

removal of coyotes is employed during winter in an effort to maximize coyote detection through snow tracking in remote and often difficult to access areas (Wagner 1997). This results in a temporal mismatch between the timing of removals in winter and the phenology of deer parturition in summer, a critical period of risk for fawns (*i.e.,* eight-weeks post-parturition; Freeman 2014), and is a sufficient period of time for immigration and replacement of coyotes to occur in some systems (Conner, Ebinger & Knowlton 2008). However, this timing of removals may negatively impact reproductive output in coyotes (Seidler, Gese & Conner 2014) by disrupting pair formation and copulation (Gantz & Knowlton 2005). Therefore, winter removal strategy assumes that a reduction in coyote abundance and/or the number of reproductive packs persists through mule deer parturition several months later, thus reducing predator-related additive mortality in fawns, due in part to reduced caloric demand with the reduction of dependent young in coyote packs (Till & Knowlton 1983; Bromley & Gese 2001).

Although temporal mismatch is likely important, spatial context is almost always known. Here we demonstrate a conceptually intuitive approach to quantifying spatial match between management removals and objectives. Specifically, we use data from a predator control study in Utah, USA to assess the spatial match between coyote (*Canis latrans*) aerial removal risk and mule deer (*Odocoileus hemionus*) resource selection during parturition using a spatially explicit, multi-level Bayesian model. Given that coyote and parturient deer resource selection, as well as aerial removal risk in coyotes, are inherently spatial processes with probabilities of use linked to landscape features, we adopt a resource selection framework for each level within the overall model (Manly *et al.* 1993). For example, mule deer exhibit distinct resource selection patterns during

parturition (Long *et al.* 2009; Freeman 2014), leading to spatial heterogeneity in the accessibility of fawns to coyote predation. Similarly, coyote removal risk is a product of encounter probabilities (*i.e.*, probability of use by coyotes) and spatial constraints acting on removal crews (*i.e.*, terrain). Thus, the efficacy of such strategy is dependent upon the degree to which removal risk overlaps mule deer habitat selection during parturition. Therefore, we evaluated the spatial match between aerial removal risk in winter for coyotes and deer probability of use during parturition at two scales, the management unit and the individual animal level (*i.e.*, home range), in order to capture the spatial-dependency associated with assessments of the predator control. In doing so, we improve our understanding of predator management impacts, while providing an objective approach to evaluating the efficacy of specific proposed management strategies.

Materials and Methods

STUDY AREA

We monitored aerial removal of coyotes, as well as space use by coyotes and mule deer, in a 1,200-km^2 area on Monroe Mountain, Fishlake National Forest, Utah (Fig. A1). The study system is highly heterogeneous and characterized by a diverse array of elevation-dependent cover types that reflect differences in seasonal moisture regimes. The elevation ranges from 1430 to 3400 meters with lower elevations dominated by shrublands (*Artemisia spp.* and *Chrysothamnus spp.*), mid-elevations by pinyon (*Pinus edulis*), juniper (*Juniperus osteosperma*), gambel oak (*Quercus gambelii*), and mahogany (*Cercocarpus ledifolius and C. montanus*), and higher elevations by alpine meadows (*Achnatherum spp.*), sagebrush (*A. tridentata*), aspen (*Populus tremuloides*), and conifer

(*Abies lasiocarpa, Pseudotsuga menziesii,* and *P. ponderosa*). Precipitation on Monroe Mountain primarily arrives in the form of snow from mid-to-late winter, with often highly variable spring mixed precipitation, late summer monsoonal rains, and dry falls.

MANAGEMENT

The USDA-Wildlife Services-Utah State Program (WS) actively implements a coyote aerial control program via helicopter and fixed-winged aircraft as a means of mitigating conflict with livestock in Utah and other western states. WS also employs these techniques as part of the current statewide deer management plan to reduce coyote predation on mule deer fawns to promote higher densities of harvestable deer (UDWR 2011, 2014). During the winters of 2012 through 2015, we capitalized on this existing plan by demarcating boundaries for WS flight teams for the purposes of overlapping with concurrent, on-the-ground data collection related to coyote and mule deer demography (Fig. A1). While not directly relevant to the current paper, we imposed a before-after control-impact design (BACI) where removals were limited to one of two areas representing the northern and southern halves of Monroe Mountain (Fig. A1). WS conducted removals on the northern site during the winters of 2012 and 2013, and the southern site during the winters of 2014 and 2015. The teams followed standard protocols, which aim to maximize removal efficacy within the logistical constraints of aerial removals (*e.g.,* aircraft/personnel availability and weather). The frequency and timing of removal flights were dependent upon weather and usually occurred within 48 hours of fresh snowfall, which facilitated coyote tracking by flight teams and is perceived to maximize efficiency of aerial removal. Flight teams reported the locations of all

animals removed using an on-board global positioning system (GPS), permitting field personnel access to carcasses from the ground.

We live-captured coyotes and fitted individuals with VHF or GPS collars (*n* = 43; Lotek GPS 6000S) using a combination of helicopter net-gunning, leg-hold traps, and neck-type cable restraints (USDA-NWRC IACUC: QA-1907, USU: IACUC-2182). We programmed GPS collar fix rates for eight-hour intervals during the non-summer season (September – May) and three-hour intervals for the summer season (June - August). We assessed resource selection in coyotes using GPS-collar data collected during periods when individuals were at risk of aerial removal (diurnal fixes from December through March). We captured female mule deer using helicopter net-gunning and fitted individuals with GPS collars during the first week of March in 2012 and 2013 (*n* = 21; Advanced Telemetry Systems models G2110D and G2110E) and again in March 2015 (N=57). We programmed collars to obtain locations at three (2013) or 11 hour intervals (2015), year-round.

MODEL FRAMEWORK

We used a hierarchical Bayesian modeling framework to simultaneously evaluate coyote resource selection, coyote removal risk, and overlap with summer resource selection by deer (Fig. 2.1). Although computationally intensive, using a multi-level framework helped to account for parameter uncertainty within nested models. We built all models in R (v3.3.1, R Core Team 2016) using *rstan* (v2.11.1, Stan Developement Team 2015; Appendix A-I).

SPATIAL DATA AND SUB-MODEL SPECIFICATION

We incorporated several ecologically relevant spatial covariates in our sub-models (Table A1), each of which was hypothesized to influence species-specific resource selection or coyote vulnerability to aerial removal. We incorporated distance to tertiary roads (*i.e*., unpaved roads) given the established influence of this variable on resource selection of both species (Rost & Bailey 1979; Arjo & Pletscher 2004; Benson, Mahoney & Patterson 2015). We did not include primary and secondary roads (i.e., paved roads and highways) as these were almost entirely limited to the margins of the study system, and therefore confounded by elevation and potentially edge effects. In addition, we included distance to point and linear water features given the relevance for large mammals in semi-arid systems (Harris *et al.* 2015), but also as a means of facilitating travel for canids during the winter (Crête & Larivière 2003). We derived landcover from LANDFIRE (LANDFIRE 2012) and simplified cover classes into aspen, other hardwood (*e.g., Quercus* spp. and *Cercocarpus* spp.), shrublands, grasslands, pinyon or juniper, other conifer, mixed hardwood and conifer, and rocky/barren (see Table A1). We then estimated distance to the nearest pixel for each landcover class at a 30-meter resolution. We used two terrain ruggedness metrics: vector ruggedness (VRM; Sappington *et al.* 2007) and terrain ruggedness index (Riley, DeGloria & Elliot 1999). We estimated each ruggedness metric and categorical aspect (*i.e.*, North, East, South, West, and flat aspect) from 30-m USGS digital elevation maps (DEM; Utah Mapping Portal, 2015). We measured summer maximum normalized difference vegetation index (NDVI) as an index of forage quality potential at a 500-meter resolution (Stoner *et al.* 2016). We assessed all continuous metrics for problematic correlations using a combination of Pearson's R (R <

0.70) and variance inflation (VIF < 4) by means of the R package *usdm* (Naimi 2015). We standardized (*i.e.*, centered by means and scaled by one standard deviation) all continuous metrics to improve model convergence. Finally, any new data used for extrapolation was truncated by the minimum and maximums derived from the dataset used in model fitting, as well as standardized by the original means and standard deviations, in an effort to limit our inference to the range of values evaluated.

We used a mixed-effect logistic model to assess the relative probability of use by coyotes following a used/available design. We used all diurnal fixes from coyote location data between December through March, corresponding to periods when coyotes were at risk of aerial removal. We quantified selection within home ranges (*i.e.*, 3rd order selection; Johnson 1980) to identify relative probability of encounter by management specialists. We generated home ranges for each GPS-collared individual by winter year using a kernel density estimator (KDE, 95% isopleth) with plug-in bandwidth estimation in R (R package *KernSmooth*; Wand & Ripley 2013). We compared used points with available points that were generated systematically within each home range at the minimum resolution of our landcover layer (30-m) following Benson (2013). The model included random effects of individual crossed with year, as well as fixed effects for the distance to existing vegetation type, terrain ruggedness (VRM), distance to roads, distance to water, and aspect.

We assessed coyote removal risk using mixed-effect logistic regression. However, in this case, the locations where removals occurred were compared to areas where removals did not occur, which we systematically sampled (30-m pixels) from within the study area (*i.e.*, removal) boundaries provided to WS. As aerial removal risk is likely

influenced by coyote resource selection, we simultaneously fit coyote resource selection with removal risk. Thus, we estimated the relative probability of coyote use from the marginalized (*i.e.*, population-level) resource selection model during each Monte Carlo iteration for inclusion as a covariate in the removal risk sub-model. The removal model included a random effect for study area crossed with year, as well as fixed effects for distance to tree cover greater than 50% (LANDFIRE 2012), ruggedness (TRI), aspect, and the relative probability of use by coyotes as derived from the coyote resource selection model.

We evaluated mule deer resource selection at the study area scale (*i.e.*, 2nd order selection; Johnson 1980) to capture the seasonal, elevation-dependent migration typical of mule deer populations in much of the western US (Merkle *et al.* 2016) and to identify areas favored by post-parturient deer. Deer location data were limited to periods representative of summer ranges (*i.e.,* timing of parturition) and specifically to periods when fawns were most at risk from coyote predation (up to eight weeks post-parturition, Freeman *et al.* 2014), corresponding to approximately June through August. We retained data from only those females that were gravid at the time of capture, survived through the middle of the following summer, and were most likely to have dependent fawns during the anticipated window for parturition (Freeman *et al.* 2014). We confirmed females were with fawns either visually during summer of each year or classified as having dependent young based on site fidelity and movement patterns using the program rASF (Mahoney & Young 2016). We further truncated an individual's data to include only those locations collected between the estimated birth dates and eight-weeks post-parturition. Using these locations, we generated individual home ranges by KDE with an 'h-ref' bandwidth

estimator in R package *adehabitatHR* (Calenge 2006). We used a different bandwidth estimator for deer than for coyotes due to differences in fix interval and movement distributions. The 'h-ref' bandwidth estimator produced more representative and less patchy home ranges for deer than did the 'plugin' estimator. We then systematically sampled (30-m) 'used' points within the 80% isopleth to reduce the influence of several infrequent yet apparently spurious locations generated by collars with longer fix intervals. We represented availability, or potential sites where deer could have established summer fawning home ranges, by sampling points systematically within a minimum convex polygon encompassing all deer points and a 15-kilometer buffer. We then compared these home ranges during parturition with population-level availability using mixed-effect logistic regression (*i.e.,* 2nd order selection; Johnson 1980). We included a random effect of year, and fixed effects for distance to landcover, distance to roads, distance to water, max NDVI, ruggedness (VRM), and aspect.

While our approach for sampling 'available' spatial data represents a census of availability at our finest spatial resolution (30-m), the increased computation required within a Bayesian framework necessitated subsetting these data in most cases. Thus, we evaluated the influence of systematic subsamples (*e.g.*, every 2+ pixels) on our representation of availability within each sub-model (Northrup *et al.* 2013; Paton & Matthiopoulos 2016). We retained the smallest sample that was representative of the 'census' or that produced manageable model fitting times, whichever was achieved first.

MODEL EVALUATION

We used approximate leave-one-out cross validation (LOOCV) and LOO

information criterion (LOOIC) to assess absolute and relative model fit, respectively (R package *loo* v0.1.6; Vehtari, Gelman & Gabry 2016). We implemented model selection within each sub-model independent of the overall multi-level model in an effort to simplify the selection process at later steps. We incorporated the single best models for both deer and coyote resource selection based on LOOIC in the multi-level removal risk model. In all cases, we confirmed proper model convergence with R-hat estimates less than 1.1, Monte Carlo errors at least one order of magnitude smaller than mean estimates, and through trace diagnostics for all model parameters (*i.e.*, 14 chains with 450 iterations and a 300-iteration warmup). In addition, we confirmed all Pareto shape parameters (k) were less than 0.5 to ensure unbiased approximations of LOO (Vehtari, Gelman & Gabry 2016). Finally, we performed posterior predictive checks for the final model by plotting observed against model predicted values (Gelman, Meng & Stern 1996).

MODEL SYNTHESIS

To address the question of scale in predator control, we generated posterior predictions for the probability of coyote removal and summer deer use for each 30-m pixel across the management unit (UDWR Monroe, Unit 23). We estimated congruence between posteriors using the Earth Mover's Distance (D_{EM}) in R package *emdist* (Urbanek & Rubner 2012), and weighted congruence to favor locations with a high median probability of use by deer (P_{Deer}) using eqn. 1.

$$\text{Eqn. 1: } C = \frac{P_{Deer}^2 * D_{EM}^2}{P_{Deer} * D_{EM}} * 1000$$

At the level of the management unit, we performed a post-hoc assessment using generalized additive models (GAMs) with Gamma errors to evaluate the influence of

elevation, ruggedness, and distance to tree cover on the weighted congruence metric, while accounting for spatial autocorrelation with isotropic thin-plate smooths (R package *mgcv*; Wood 2011). At the level of the individual, in cases where collared animals were removed, we estimated the median and coefficient of variation (CV) in weighted congruence across all 30-m cells within a coyote's home range. For those removals lacking home range data, we generated biologically-meaningful buffers around removals by simulating home ranges with a hidden Markov model fitted to the complete coyote GPS dataset (R package *moveHMM*; Michelot, Langrock & Patterson 2016) and with covariates for time between fixes and residency. We generated a 1000 home ranges per removal using minimum convex polygons (Moorcroft, Lewis & Crabtree 2006; Van Moorter *et al.* 2009), each derived from a single simulated trajectory of 100 locations. We then used these simulated home ranges to derive a posterior expectation of median weighted congruence for each individual, which in turn can be interpreted as the degree to which that individual overlapped mule deer parturition habitat and the potential contribution of that individual towards mule deer management objectives.

Results

COYOTE RESOURCE SELECTION

We used GPS data from nine individuals (Fix Success: $\mu = 94.1\%$, $\sigma = 3.5\%$) with sufficient location information during the winter at risk period, resulting in 16 seasonal home ranges from nine different packs. We evaluated 26 models for coyote resource selection, including a single null fixed effects model (Table A2). We did not consider models with aspen due to problematic correlations with distance to conifer and mixed

conifer/hardwood.

Here, we derive inference from the most parsimonious top model (Table 2.1, Fig. 2.2a), which was also our best model based on LOOic (Table A2). During daylight hours in the winter, coyotes selected for shrublands, rocky/barren cover, and water, as well as intermediate distances to grasslands and tertiary roads. They also selected rugged terrain, and east and south-facing aspects (relative to north aspects). Coyotes avoided conifer, mixed conifer/hardwood, and non-aspen hardwood stands.

COYOTE REMOVAL RISK

A total of 182 coyotes were removed from the study site over four years. We received removal locations for 156 of these and visited 106. The remaining 50 removal sites were either inaccessible due to winter conditions, had been covered by consecutive snowfalls, or sufficient time had transpired permitting scavengers to disperse the carcasses. The accuracy of aerial fixes was consistently within 50 meters, indicating that the GPS error was usually less than our minimum spatial data resolution. For the removal risk model, we selected variables hypothesized to influence the detectability and accessibility of coyotes to aerial removal. Thus, we included aspect given its relationship with snow cover, and therefore tracking conditions, attributable to variable sun exposure throughout much of the winter. In addition, we included relative probability of use (as estimated from the top coyote resource selection model), distance to dense tree cover, and terrain ruggedness (TRI). We used TRI, as opposed to VRM, given the collinearity with slope, which we also anticipated influenced accessibility by pilots and is thus a more parsimonious way of capturing the same desired terrain effect.

We evaluated seven models for coyote removal risk and derived inference from the single best model (Table 2.1, Table A3, Fig. 2.2b). In general, aspect did not influence coyote removal risk. However, coyotes were most susceptible at intermediate distances to tree cover. In addition, coyotes were much more likely to be removed in flatter terrain (Fig. A2). The nonlinearity for TRI indicated that the probability of coyote removal declined exponentially with increases in ruggedness. While not significant due to high uncertainty, the large effect of probability of use indicated that managers were removing animals from areas where encounter probabilities are high, namely, open, flat terrain.

DEER RESOURCE SELECTION

We had sufficient location data from 39 adult female deer with confirmed or probable dependent young from 2012 through 2015, resulting in a total of 51 summer home range estimates. Of these 51 probable fawning events, we confirmed six visually and estimated 45 using program rASF. However, rASF was less precise for some individuals with the longer fix interval collars deployed in 2015 (*i.e.*, two- to seven-day window). Thus, when fawning was confirmed as likely, we used the first day of the estimated parturition interval as the birth date for truncating location data. Eleven of these females (14 home ranges) summered on neighboring ranges outside the Monroe Mountain management unit. However, these ranges are also districts in Fishlake National Forest and consisted of a similar mosaic of landcover types and plant assemblages. Thus, the added power provided by these additional individuals increased the representative nature of deer site selection during parturition for the region. Our sample of availability

encompassed all lands that were potentially accessible to study animals, including these neighboring ranges, for the deer selection models only.

We evaluated 23 models for deer resource selection (Table A4). LOOic strongly supported our top model for adult deer resource selection during the 8-weeks post-parturition (Fig. 2.2c), indicating significant non-linearities in all our continuous metrics except for distance to conifer (Table 2.1). The top model indicated that deer selected fawning sites near tertiary roads, shrublands, aspen, conifer, or hardwood, as well as intermediate levels of ruggedness (VRM) and NDVI. Deer avoided grasslands, pinyon-juniper, and water when selecting fawning sites. In addition, deer selected for home ranges on east-, south-, and north-facing aspects over west-facing and no aspect.

CONGRUENCE AT THE LEVEL OF THE MANAGEMENT UNIT

All three sub-models exhibited good posterior predictive accuracy (Fig. A2). The study-area median congruence between coyote removal risk and deer fawn site selection, after weighting by mule deer probability of use, was 0.25 (CV = 120.51) (Fig. 2.3). The GAM indicated substantial spatial variation in weighted congruence between removal risk and probability of use by deer (spatial smooths with edf=1446.06, Fig. A3a). We tested models with elevation, ruggedness (TRI), and elevation with ruggedness. Model selection retained elevation (edf=37.97) and ruggedness (edf=39.83). However, the effect of elevation is not likely to be biologically meaningful given the relatively flat relationship (Fig A3c). Yet, congruence declines precipitously and non-linearly as ruggedness increases (Fig A3b).

CONGRUENCE AT THE LEVEL OF THE INDIVIDUAL REMOVAL

The hidden Markov models performed well at simulating movement trajectories, and thus home ranges, when fitted using coyote GPS trajectories (Fig. 2.4a). Simulated home range sizes were slightly larger than observed, but in general median home range size from simulations matched our observed sizes in cases where home ranges were known (Fig. 2.4b). In addition, median overlap with predicted relative probability of use by deer was also a close approximation for the observed values in known coyotes and in all cases were encompassed by the 95% highest posterior density interval (Fig. 2.4c and Table A5). Output from this comparison can provide individual estimates of potential overlap with management objectives (*i.e.*, deer resource selection during parturition) (Fig. 2.5 and Table A5).

Discussion

Our primary objective was to highlight a quantitatively evaluate the spatial match between management actions and objectives. In the western US, Coyote management is often implemented as a means of mitigating presumed additive mortality in mule deer fawns. However, it remains unclear whether coyotes are able to regulate or limit mule deer populations (Ballard *et al.* 2001; Hurley *et al.* 2011). This ambiguity is at least partially attributable to highly heterogeneous landscapes, spatially and temporally variable management effort, and variation in location and status of individual coyotes removed. To our knowledge, these spatial factors have never previously been accounted for in an assessment of predator control.

We demonstrate the use of a multi-level Bayesian model to evaluate the spatial match between predator management actions relative to site selection in gravid deer

during the fawning season. We incorporated winter diurnal resource selection in coyotes (3rd order selection) as a measure of the relative probability of encounter by WS in our removal risk sub-model. In addition, we included covariates that hypothetically influence the 'accessibility' of coyotes to aerial removal, specifically distance to tree cover, terrain (TRI), and aspect. Similarly, we evaluated adult deer resource selection or summer site selection (2nd order selection) during the eight weeks post-parturition, the period when fawns are most at risk from coyote predation (Freeman 2014). In general, our model, and the respective sub-models, accurately captured coyote (Arjo & Pletscher 2004) and deer resource selection (Long *et al.* 2009), as well as coyote removal risk, and exhibited strong predictive inference based on posterior predictive checks (Fig. A3).

Although intuitive, our model indicated that coyotes were generally most at risk of removal in areas with the highest predicted (relative) probability of occurrence, which was represented by open shrublands in low to moderately rugged terrain during the daylight hours in winter. However, after accounting for coyote resource selection, there appeared to be spatial constraints acting on the efficacy of removal, indicating coyote removal risk declined as ruggedness increased or when near tree cover. Likely, flight crews were impeded by more rugged terrain due to safety concerns, requiring more attentive flying by the pilot and overall reduced detectability of coyotes. Although trees pose a similar safety concern, tree cover limits visibility and obstructs projectiles used in lethal removal, thereby providing refuge for coyotes. Our models also indicated a decline in removal risk at higher distances to tree cover, suggesting intermediate distances were most risky for coyotes. Intermediate distances are likely an artifact of WS targeting areas believed to be favored by mule deer or due to differences in coyote behavioral response

to aircraft affecting detectability as distance to cover increases (*e.g.*, flight response near tree cover versus holding still when far from cover). There was no effect of aspect, at least relative to our expectations of coyote resource selection. This is not particularly surprising given the timing of flights to coincide with fresh snowfall (*i.e.*, before south faces had an opportunity to melt off). Nonetheless, this clearly highlights the spatial heterogeneity in coyote aerial removal risk and emphasizes the constraints acting on aerial removals as a management tool for mule deer (Knowlton & Windberg 1985).

We recognize that detection and effort are likely key predictors of absolute removal risk, but we could not explicitly account for these factors. However, our results are robust within the context of our primary objective, in that we compare spatial congruence between removal risk and parturient deer resource selection. For example, increased removal effort will lead to a proportional increase in the relative probability of risk but will not change the spatial context of risk (*i.e.,* low risk will remain low risk and *vice versa*). Therefore, our estimates of spatial congruence between removal risk and parturient deer resource selection should also be consistent regardless of effort, though the absolute measures of congruence will change. Similarly, we acknowledge that although animals were likely detected and pursued before ultimately being removed, initial encounter is a matter of detection. Documenting where an animal was removed with precision was more reflective of actual risk and therefore most relevant to our analytical goals. However, the hierarchical structure of the risk model helped to capture variation between years and across study areas that is likely attributable to variation in detection, density, and climatic conditions.

When considering the spatial overlap between coyote removal risk and deer

resource selection, a similar relationship manifests as the one observed in the coyote removal risk sub-model. We evaluated the influence of elevation and ruggedness on the spatial congruency between management action and objective. These models clearly suggest no effect of elevation and a strong negative non-linear effect of ruggedness on weighted congruency (Fig A3), indicating coyotes occupying flat and open terrain at higher elevations are just as susceptible to removal risk. Thus, not surprisingly, WS performs well at matching objectives in areas with low ruggedness (white colors in Fig. 2.2b/c & 2.3). However, declines in overlap are also indicative of differences in expectations of space use in both species, with coyotes generally preferring more open landcover classifications (*e.g.*, barren-ground and shrublands) relative to mule deer (*e.g.*, forest) (Table 2.1).

In addition to assessing match at the scale of a management area, we provide a means of quantifying potential impact at the level of the individual removal by simulating home ranges through fitted hidden Markov movement models. By intersecting the simulated home ranges with deer probability of use during parturition, we can then derive a posterior expectation of overlap on a per removal basis. Doing so clearly demonstrates that not all removals are equally effective with regards to objectives (Fig. 2.5; Mitchell, Jaeger & Barrett 2004), suggesting the need to weight actions by their potential impact in a spatially explicit manner when evaluating the efficacy of a given management strategy.

We also recognize that there are likely seasonal differences in coyote resource selection and resource selection (Koehler & Hornocker 1991; Neale & Sacks 2001). By evaluating winter diurnal resource selection, we intended to address the issue of encounter probability during removal efforts, and therefore seasonal differences are likely

of little consequence. However, with regards to simulating home ranges based on winter removal locations, there is ample evidence to indicate that coyotes in the region are non-migratory and exhibit strong home range fidelity across seasons (Gantz & Knowlton 2005). In addition, we parameterized our hidden Markov models using the complete year-round location datasets, including both resident and transient individuals. Thus, our estimates of individual-level impact should be conservative.

Prior predator control studies have often assumed each management removal is equally impactful to the desired objectives (*e.g.*, Hurley *et al.* 2011). We highlight substantial spatial variation in the efficacy of a given action in relation to the desired objective. We demonstrate that the outcomes of a given management strategy (*i.e.*, aerial control of coyotes) can be highly variable in heterogeneous landscapes at two distinct spatial scales. First, aerial control is likely to be inconsequential in regions where overlap with the focal species is low while potentially more impactful in other regions where aerial risk is congruent with management objectives. Second, we demonstrate a means of quantifying the potential impact of individual removals such that the next logical step will be to assess fawn survival in a spatially explicit context (Fig. 2.3). Otherwise, we anticipate that important spatial variation will likely bias our ability to accurately evaluate the efficacy of predator control programs (Stoddart, Knowlton & Taylor 1989). For example, although the annual number of coyotes removed was consistent from year to year, coyotes removed during 2015 were predicted to be largely ineffective due to poor of overlap with parturient mule deer resource selection (Fig. 2.5) and could lead to erroneous conclusions about the efficacy of predator control in the absence of spatial context. We also provide a means of quantifying and contrasting potential management

impact across multiple management areas. When used in conjunction with other relevant metrics (*e.g.,* estimated deer population growth), managers can implement these spatial assessments to determine which management areas are most conducive to coyote aerial removal and most likely to be effective in terms of overlap with mule deer fawning sites. One could also extend these efforts to evaluate fluctuations in mismatch in temporally dynamic environments. In our case, we experienced mild winters and relatively robust growth in deer and alternative prey populations (*e.g.,* lagomorphs and other small mammals), which could have contributed to reduced efficacy in removal efforts and a lower expectation of spatial overlap in coyote and deer resource selection. With limited operating budgets, managers can make objective decisions about where and when proposed management actions should be employed, while reducing risks to human safety, unnecessary animal removals, and undue financial burden to wildlife programs.

The ambiguity regarding management impacts is not reserved to predator control alone. The importance of spatial context in wildlife management is increasingly relevant. The growth in popularity associated with resource selection functions, such as the generalized linear mixed models implemented here, is a testament to such a focus (*e.g.*, Johnson *et al.* 2006; Gillies *et al.* 2006). Thus, we should not expect all management actions to result in equivalent effects when operating in a highly heterogeneous environment. Hierarchical models lend themselves well to exploring complex interactions across multiple datasets or spatial scales, particularly when there is need to account for variation and uncertainty at the respective levels (Gelman *et al.* 2014). While the methods outlined here represent only one of many potential approaches, such models can be extended to evaluate the match between management action and objectives in a variety of

circumstances where space is an important driver of management success. For example, we recognize the potential value in considering such models within the context of restoration ecology (*e.g.*, riparian restoration or animal reintroductions), habitat management (*e.g.*, landcover modification or enhancement), or population regulation (*e.g.*, ungulate management to reduce overbrowsing/grazing). By integrating resource selection data as we do here, or through incorporating demographic data, we can begin to quantify the relative impacts of spatially explicit management actions so that we may arrive at an unbiased understanding of impacts and improved efficiency through more targeted efforts.

Authors' Contributions

PM lead the writing. PM and JY conceived the idea and methodology for the analysis, as well as collected the coyote data. DS, RL, and BM collected the deer data. All authors contributed to the drafts and gave final approval for publication.

Data Accessibility

Data and code will be made available on GitHub with an associated DOI should the article be accepted for publication.

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Tables and Figures

Table 2.1. Coefficient estimates for the coyote resource selection, coyote removal risk, and deer resource selection models. Lower and upper CI are the lower and upper 95% credible intervals. PJ represents pinyon and juniper cover and VRM the vector ruggedness metric. *Reference groups are north aspect for deer and coyote resource selection and north, west, and no aspect for removal risk.

	Coyote Resource selection (3rd Order)				Coyote Removal Risk				Deer Resource selection (2nd Order)			
Fixed Effects	**mean**	**SD**	**Lower CI**	**Upper CI**	**mean**	**SD**	**Lower CI**	**Upper CI**	**mean**	**SD**	**Lower CI**	**Upper CI**
Dist. to Aspen									-0.102	0.028	-0.156	-0.047
Dist. to Aspen^2									-0.054	0.020	-0.094	-0.014
Dist. to Barren	-0.052	0.024	-0.096	-0.004								
Dist. to Conifer	0.181	0.036	0.110	0.252					-0.560	0.033	-0.625	-0.496
Dist. to Grass	-0.080	0.039	-0.157	-0.004					0.471	0.017	0.439	0.504
Dist. to Grass^2	0.072	0.021	0.032	0.111					-0.130	0.009	-0.148	-0.114
Dist. to HW	0.177	0.032	0.113	0.240					-0.360	0.020	-0.401	-0.320
Dist. to HW^2	-0.050	0.014	-0.078	-0.024					-0.078	0.016	-0.110	-0.047
Dist. to Mix	0.059	0.050	-0.039	0.159								
Dist. to PJ									0.730	0.025	0.680	0.779
Dist. to PJ^2									-0.262	0.009	-0.279	-0.244
Dist. to Roads	0.068	0.031	0.008	0.129					-0.258	0.014	-0.286	-0.230
Dist. to Roads^2	-0.062	0.015	-0.092	-0.032					0.043	0.004	0.035	0.051
Dist. to Shrub	-0.106	0.025	-0.156	-0.057					-0.050	0.018	-0.084	-0.014
Dist. to Shrub^2									-0.013	0.005	-0.023	-0.003
Dist. to Tree Cover (>50%)					-0.036	0.121	-0.281	0.195				
Dist. to Tree Cover^2 (>50%)					-0.402	0.124	-0.664	-0.179				
Dist. to Water	-0.118	0.023	-0.163	-0.075					0.575	0.015	0.545	0.604
Dist. to Water^2									-0.270	0.013	-0.297	-0.244
Max NDVI									1.056	0.026	1.005	1.108
Max NDVI^2									-1.099	0.021	-1.140	-1.058
Ruggedness, TRI					0.461	0.139	0.180	0.734				
Ruggedness, TRI^2					-0.216	0.077	-0.368	-0.070				
Ruggedness, VRM	0.063	0.020	0.024	0.103					0.078	0.012	0.054	0.102
Ruggedness, VRM^2									-0.035	0.011	-0.056	-0.014

Table 2.1 cont.

Prob. Of Use by Coyotes					1.436	1.938	-2.044	5.567				
East*	0.195	0.058	0.078	0.306	0.145	0.204	-0.267	0.535	0.357	0.027	0.305	0.409
South*	0.247	0.060	0.130	0.363	0.126	0.229	-0.336	0.559	0.056	0.030	-0.002	0.115
West*	-0.277	0.058	-0.392	-0.165					-0.377	0.028	-0.432	-0.323
No Aspect*	0.260	0.456	-0.708	1.074					-0.451	0.102	-0.653	-0.258
Random Effects												
(RE) Year sd									1.647	0.951	0.696	4.257
(RE) Year mean									-1.480	0.956	-3.508	0.546
(RE) Individual sd	0.687	0.216	0.402	1.198								
(RE) Individual mean	-2.234	0.247	-2.720	-1.727								
(RE) Removal Area sd					1.599	1.880	0.221	7.137				
(RE) Removal Area mean					-4.860	1.575	-7.479	-0.990				

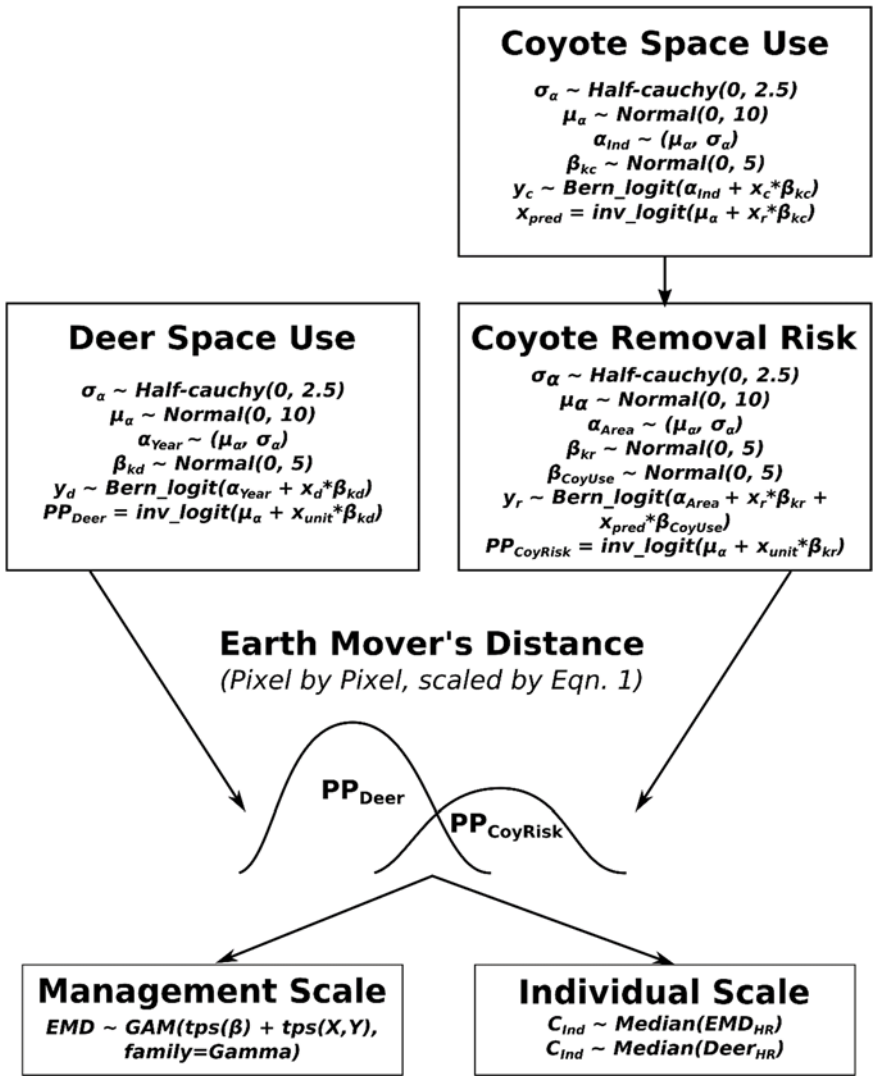

Fig. 2.1. Multi-level model specification for evaluating the spatial overlap between management actions and objectives. Each box corresponds to a dependent sub-model specification with prior distributions, hyperparameters, and model distributions ($y_{c,r,d}$). Subscripts of *c, r,* and *d* are for coyote, removal risk, and deer, respectively. Arrows represent the hierarchical flow of sub-model output during simultaneous model fitting. X_{pred} are model predicted data and PP are Pixel-by-Pixel model estimates.

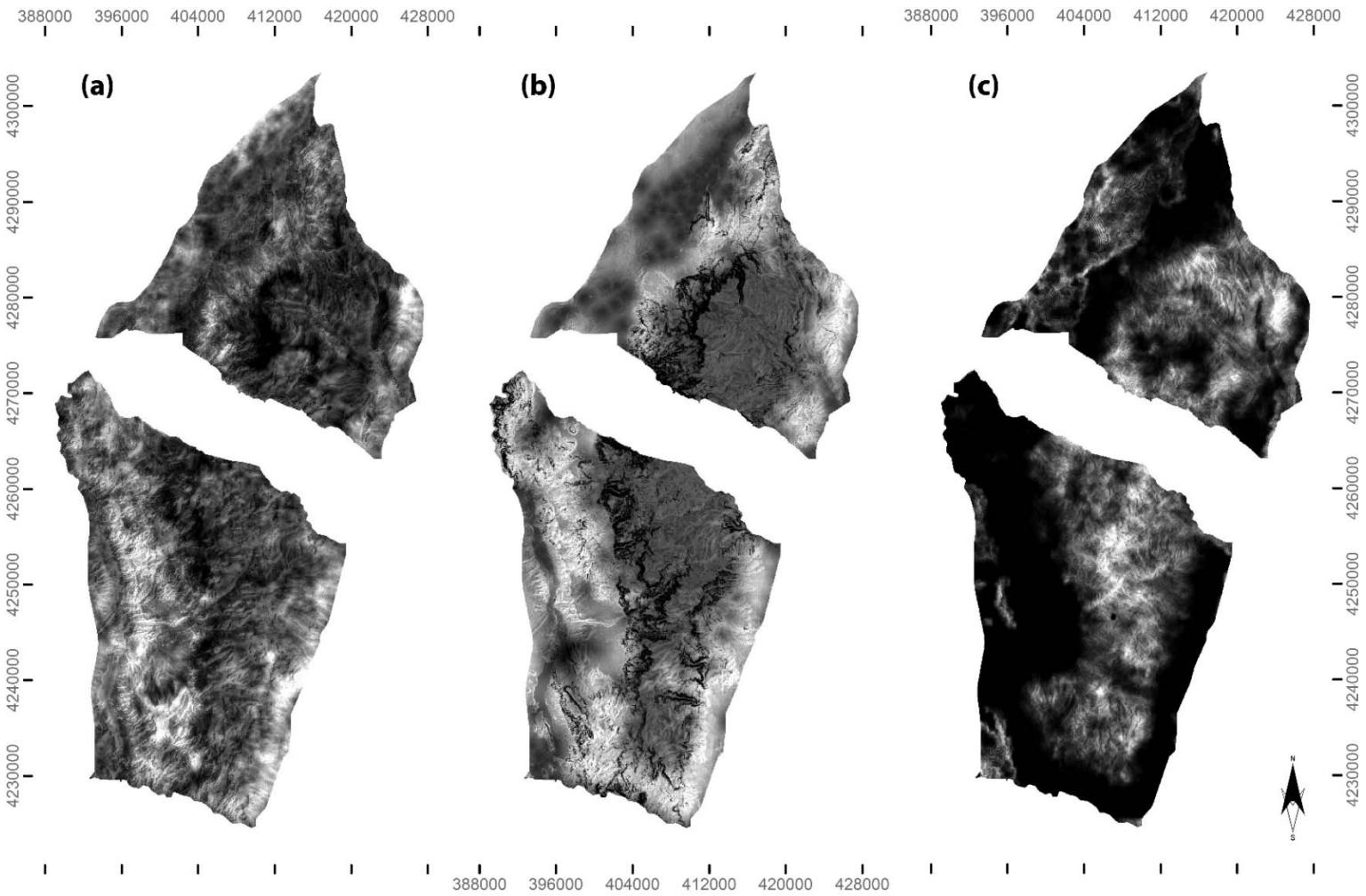

Fig. 2.2. Heat maps for the model predicted relative probabilities of coyote use (a), coyote removal risk (b), and deer use (c). Dark to light is low to high probability, respectively.

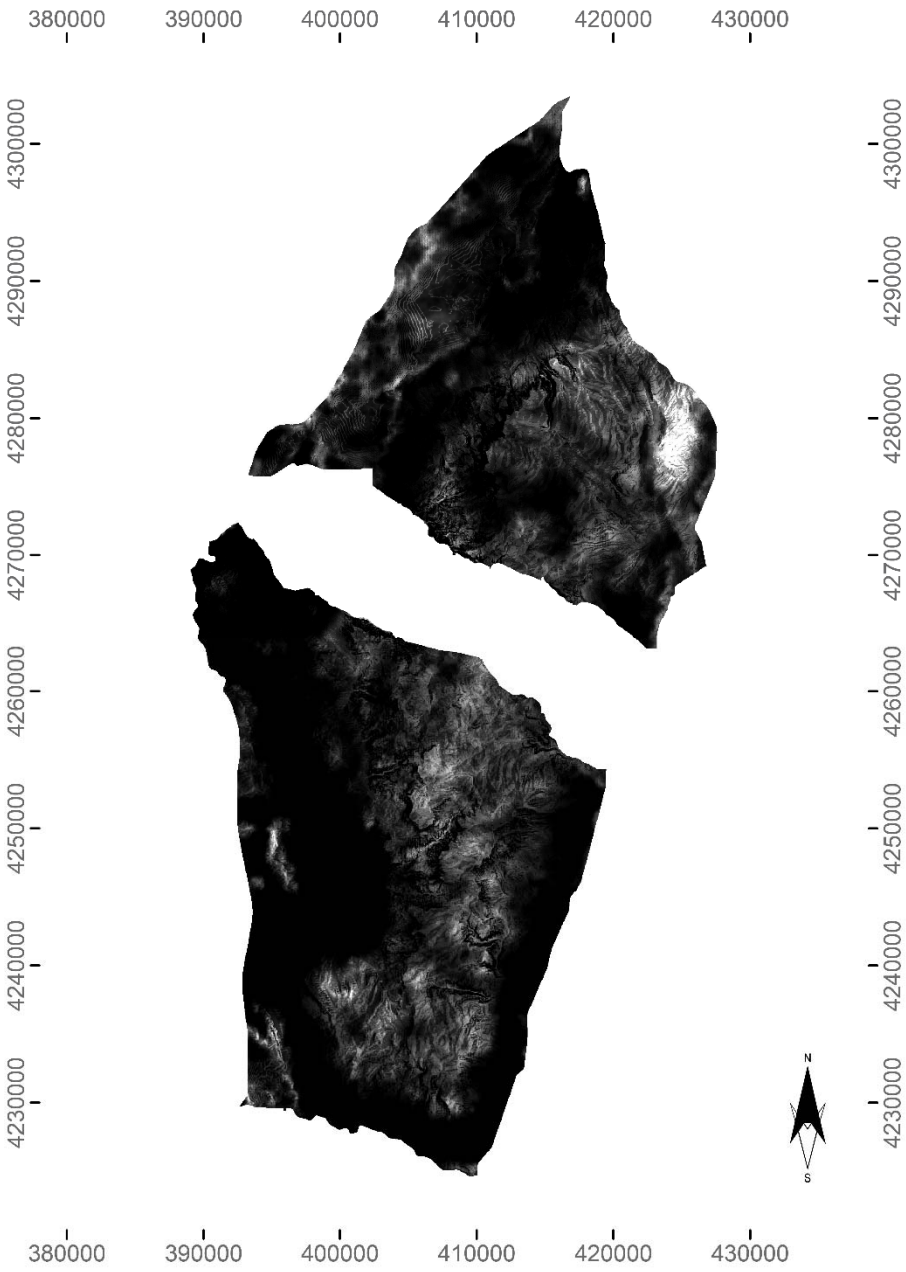

Fig. 2.3. Heat map of weighted congruence where lighter areas correspond to stronger congruency between coyote removal risk and deer resource selection in areas with higher probability of use by mule deer.

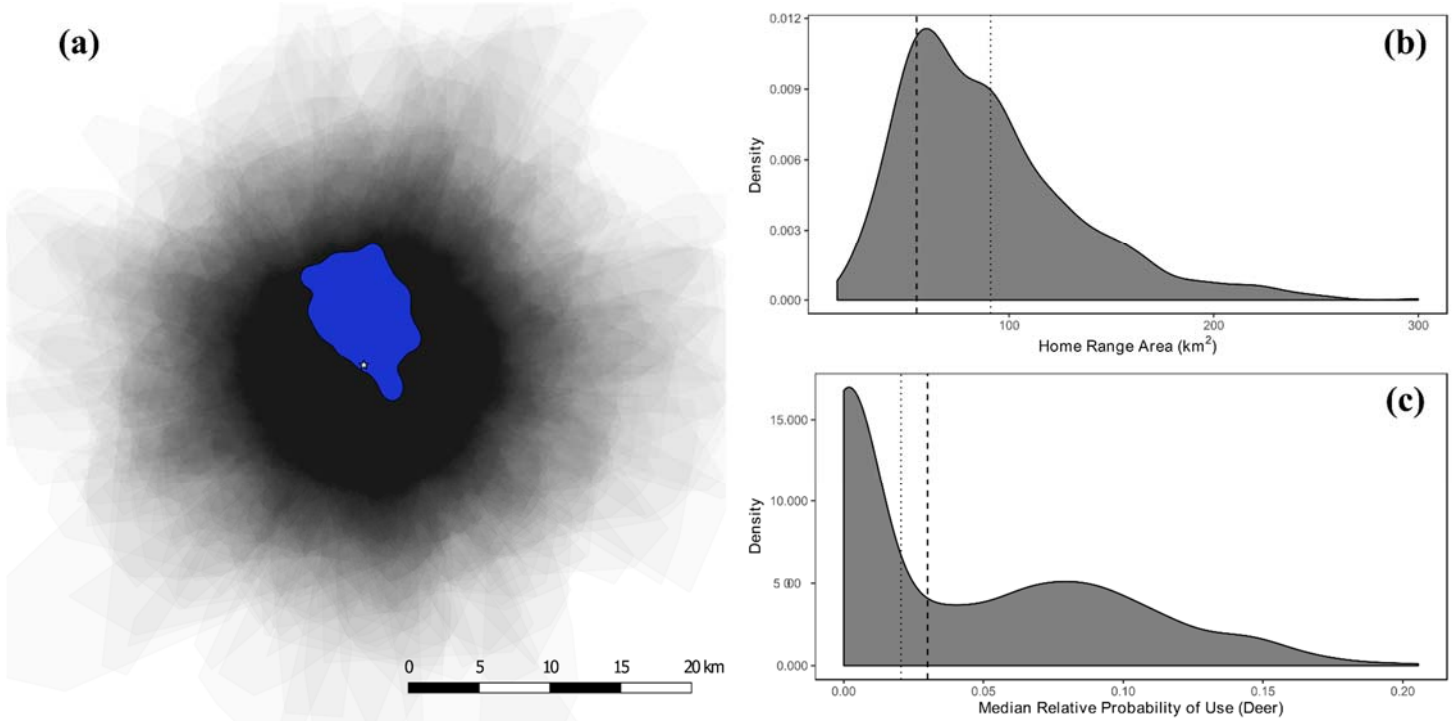

Fig. 2.4. An example of a simulated home range space (a) for a removed coyote (star) with a known home range (blue polygon). The darker shading corresponds to more frequent home range overlap in a given region of space. The densities for 1000 simulated home range areas (b) and median overlap with relative probability of use in deer (c), with observed estimates (dashed) and simulated estimates (dotted) represented as vertical lines.

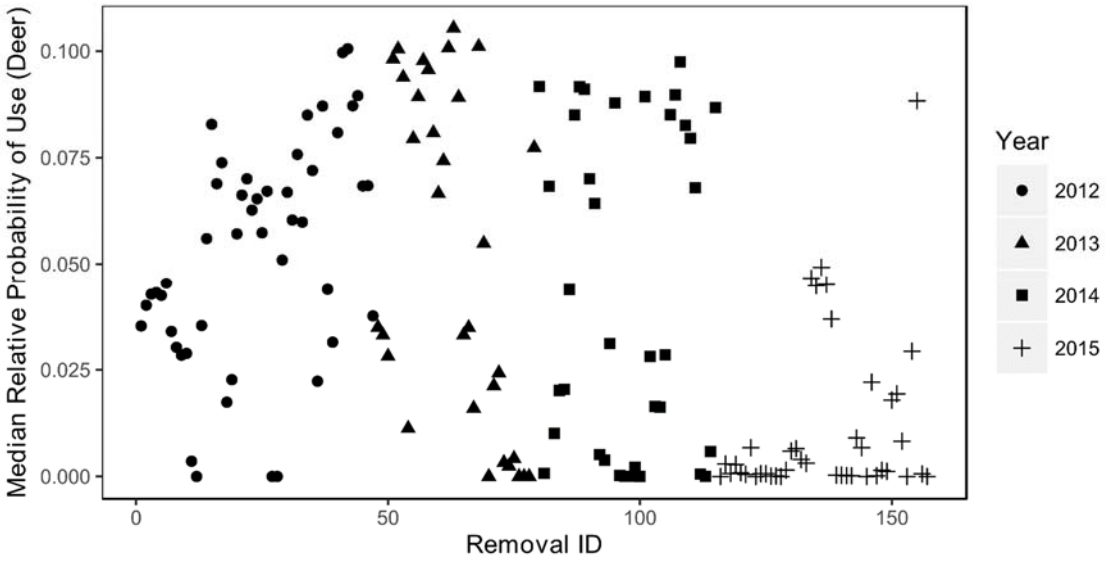

Fig. 2.5. The estimated median overlap with relative probability of use by deer for all 156 coyote removals. Larger median values indicate greater potential impact on mule populations.

CHAPTER 3

RISK VS. REWARD: THE ROLE OF INTRAGUILD KILLING AND DYNAMIC PREY RESOURCES ON MESOPREDATOR SPACE USE[2]

ABSTRACT

Species interactions are fundamental to the way animals navigate landscapes in search of resources. Yet, evaluations of resource selection are often limited to one or two interacting species. In the absence of relevant community complexity and without a keen understanding of the mechanistic drivers of space use behavior, such assessments are limited in scope and exhibit poor predictive power. Here, we investigated the motivations contributing to mesopredator space use by developing a multi-level Bayesian resource selection model with representative community complexity in the form of variable prey resources and space use in a dominant competitor. Our results indicate that western coyotes (*Canis latrans*) can balance risk of encountering cougars (*Puma concolor*) while acquiring diverse prey. Coyotes had limited access to large prey (*i.e.,* mule deer; *Odocoileus hemionus*) when avoiding the dominant competitor; however, coyotes shifted towards this riskier prey as lagomorphs declined in density. Similar patterns are likely to manifest in other systems with predator guilds and could have important implications for the way we manage and conserve species. Therefore, we encourage community-based approaches to resource selection, which will strengthen the causal link between observed patterns in space use and resources of interest.

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[2] Mahoney, P.J., D. Stoner, and J.K. Young. *Proceedings of the Royal Society B: Biological Sciences*.

1. Introduction

Understanding the fundamental motivations and consequences of animal space use is a central theme in ecology [1]. The dynamic nature of communities, as reflected by changes in the presence or density of interacting species within and across trophic levels, is likely a key determinant in how individuals navigate landscapes to acquire resources while balancing risks associated with competitor interference and encounters with predators [2]. Yet investigations of space use are typically limited to single species or pairwise interactions (*e.g.*, one predator and prey), offering limited insight and poor generality within or beyond the community studied. However, recent progress in community ecology has increasingly emphasized the importance of considering species associations (*i.e.*, community complexity) when evaluating individual space use and community processes [3,4], allowing for an improved understanding of the mechanisms underlying observed behavior and population processes.

The need to consider complexity within communities is perhaps best demonstrated when community-level interactions such as competition and predator-prey processes, work in concert with relevant abiotic factors, to influence population abundance in one or more species [5,6]. Predators have the capacity to either stabilize or destabilize prey populations [7]. Persistence of prey populations in such systems is dependent upon species' life history (*e.g.*, generalist vs. specialist predators) [8,9], the presence of competitors within one or more trophic levels [10], spatiotemporal variation in prey vulnerability [11], and resource availability [12]. Although predators differentially impact community stability and diversity, the presence of predator effects may depend on the extent to which predator and prey dynamics are coupled, as well as

the relative strength of interactions between competitors within trophic levels. For example, generalist predators can influence prey through apparent competition in systems with multiple prey species [13–15], provided sufficient plasticity in predator diet [16]. Thus, the population of one or more prey species can be suppressed when co-occurring with a predator and additional prey, even in the absence of direct competition between prey. Competition among predators (*e.g.*, intraguild predation) can induce behavioral modifications, such as partitioning of space and time, in predators of intermediate size and competitive strength through avoidance of apex predators [17,18]. This can provide spatial or temporal refugia for non-shared prey species through mesopredator suppression [19]. In the absence of apex predators, mesopredator populations may be 'released' from trophic regulation and suppress some prey populations [20,21]. Thus, predator guild dynamics can influence prey populations and community diversity [22,23].

Space use manifests as the consequence of an individual's rate of encounter with conspecifics, competitors, and predators while acquiring resources [2]. Therefore, individuals may be able to respond to dynamic shifts in the availability of space as a consequence of fluctuating predator, competitor, and prey densities [24–27]. Although Ideal Free Distribution Theory (IFD) predicts individuals within a population are distributed proportional to resource availability [28], systematic deviations from IFD, where species consistently underutilize resource-rich environments and overutilize resource-poor environments, are often explained by individual responses to predators [29], asymmetries in competitive interactions [30], and animal movement as it relates to landscape connectivity [31]. Resource selection analyses (RSA) that integrate all relevant species interactions, or alternatively community-based RSAs, provide a means of

developing a more comprehensive understanding of animal space and resource use by documenting shifts in selection as an outcome of changes in density or behavior in all relevant community species. By doing so, ecologists can improve the generality of their findings and extend the predictive power of RSAs for use in other populations, document expected use in expanding populations, or account for changes in use in response to population fluctuations in focal or competitor species.

Although originally conceptualized decades ago [25], community-based RSAs have only recently gained momentum as sufficient data become available [27,32–35]. Here, we evaluated movement and resource selection in a generalist mesopredator, the western coyote (*Canis latrans*), under dynamic prey conditions and in the presence of a dominant competitor, the cougar (*Puma concolor*). We develop a community-based, predator-prey resource selection model in an area characterized by a diverse array of elevation-dependent ecotypes that reflect differences in seasonal moisture regimes, which in turn support diverse vertebrate assemblages and thus possible prey for generalist predators. Coyotes occupy a wide variety of habitats across their range, including prairies [36], alpine forests and meadows [37], and densely populated urban centers [38,39]. As habitat generalists, coyotes are expected to favor space use patterns that maximize prey resource acquisition while balancing the demands of self-maintenance, reproduction, and exposure to risk. Coyotes are cursorial predators that predominantly hunt small mammals and lagomorphs in the southwestern U.S. [40], but can also respond to shifts in vulnerability of larger prey and consume ungulates when conditions permit (*e.g.*, mule deer fawns: *Odocoileus hemionus*) [41]. Cougars are solitary predators specializing in larger, predominantly ungulate prey (*e.g.,* mule deer). Encounters between cougars and

coyotes occasionally result in coyote mortality, typically associated with attempted kleptoparasitism by coyotes of cached cougar kills [17,42,43]. However, as ambush predators, cougars exhibit predictable space use patterns that are likely perceptible to coyotes (e.g., [42]), permitting individuals to respond to perceived risk as they move through heterogeneous landscapes.

We hypothesized that coyotes would generally select areas with high lagomorph densities and small mammal biomass over areas favored by parturient deer during summer. In addition, we expected coyotes would avoid areas that pose the greatest risk, which we modeled here as the relative probability of encountering an active cougar (*i.e.*, intraguild killing) and distance to roads (*i.e.*, anthropogenic risk). We focused our assessment on the summer months (June – August) as this was the period for which we had the highest resolution movement data for coyotes and sampled primary prey availability. Additionally, summer coincided with mule deer parturition, a period of time when fawns were most at risk from coyote predation [44]. Although we present our findings from a specific cougar-coyote-prey system in the western US, we believe our approach is broadly applicable and could be implemented in any predator-prey system with similar data. To our knowledge, this effort represents the first comprehensive assessment of resource selection by a mesopredator that explicitly integrates movement behavior of the focal species, resource selection by prey, and the potential influence of the apex predator.

2. Material and methods

(a) Animal captures and collaring

We captured and GPS collared coyotes (N=12; Lotek GPS 6000S) using a combination of helicopter net-gunning and leg-hold traps and programmed collar fix rates for eight-hour intervals outside of summer (September – May) and three-hour intervals during summer (June - August). We captured cougars with the assistance of trained hounds and houndsman. We immobilized treed cougars with Ketamine/Xylazine and deployed GPS collars (N=9; Lotek 3300, 4400; Telemetry Solutions Q4000; Advanced Telemetry Systems G2110D) with fix intervals of 3-4 hours. We captured female mule deer using helicopter net-gunning and fitted individuals with GPS collars during the first week of March in 2012 and 2013 (N=21; ATS G2110D and G2110E) and again in March 2015 (N=57). Deer collar fix rates were programmed for three (2013) or 11 hour intervals (2015). All deer were pregnant at the time of capture.

(b) Prey surveys

We conducted spotlight surveys for lagomorphs along two 50-km road transects (divided into 300-m segments), each commencing 30 minutes after observed sunset. We recorded the location of detections, species of lagomorph, and the perpendicular distance from the line transect. Surveys were conducted weekly from mid-June to the end of July for five replicates per transect per year.

We randomly generated locations for 30 small mammal sampling grids, stratified by five broad landcover classes (e.g., aspen: *Populus tremuloides*; conifer: *Abies lasiocarpa*, *Pseudotsuga menziesii*, and *P. ponderosa*; other hardwood: Quercus

gambelii, *Cercocarpus ledifolius*, and *C. montanus*; pinyon/juniper: *Pinus edulis* and *Juniperus osteosperma*; shrub/grasslands) and constrained to be ≤1 km from a road. Each grid consisted of a 5x5 array (4x5 in 2012) of Sherman traps (Models: XLK Folding and LNG12 Non-Folding) spaced 10 meters apart. We monitored each grid for three consecutive nights, with no more than three grids operating during any given block of four days. Trapping was conducted from mid-June through early August during each year of the study.

We identified cougar clusters using the R program *rASF* [45]. We defined clusters as three or more points that were within 100-meters distance and occurred within 72 hours of one another. We visited clusters and confirmed the presence and species of kill during the summer after collar data were collected and when sites were accessible.

(c) Analytical approach

We developed a hierarchical Bayesian model to investigate factors influencing space use and movements by coyotes during summer in the context of multiple prey species and spatial risk associated with cougars and human landscape use (figure 3.1; appendix B-I). We derived estimates from five component sub-models representing prey resources or risk factors hypothesized to influence coyote movement (table B1). We developed each sub-model using one or more variables hypothesized to influence the respective response variables. In cases where we sample availability (*i.e.,* second and third order RSF; [46]), we initially did so systematically at the finest resolution of our cover data (30-m) [47]. However, our samples of availability were further reduced to the smallest sample of points representative of our full systematic sample for all metrics used

in the assessment [48]. We centered and scaled (by one standard deviation) all continuous metrics to improve model convergence. We assessed chain convergence in all models using trace diagnostics and $\hat{R} < 1.1$ [49]. We further evaluated models with posterior predictive checks and leave-one-out cross-validation where appropriate [50]. We fit the overall coyote space use model using the top model from each of the independently evaluated sub-models. We conducted all modeling in program R [51] using the packages *rstan* [52] and *jagsUI* [53].

For cougars, we investigated resource selection within home ranges (*i.e.*, third order selection) in active individuals using a generalized linear mixed model with a binomial response following a used (1) - available (0) design [54]. We determined activity period from a subset of cougar GPS collars containing 2-D accelerometers (N=4). We truncated all cougar location data to include only those locations from the activity period. We estimated seasonal home ranges within each year using the complete datasets and kernel density estimators (95% isopleths) with a plugin bandwidth estimator [55]. We systematically sampled availability within each home range and paired appropriate used and available points by incorporating crossed random effects of individual and year. We used location information from known cached cougar kills, representing potential carrion subsidies, to identify the relative probability of encountering a cougar kill following a procedure akin to second order selection. Here, we sampled availability across the study area (0) and 'use' across clusters (1) systematically and evaluated these data using hierarchical logistic regression with a single random effect of year.

We analyzed lagomorph survey data using hierarchical distance sampling [56]

and tested for an effect of elevation, percent forest cover, and ruggedness on density of all lagomorphs for every 30-m pixel across the study area. We modeled detection as a hazard function with a single covariate for distance from transect (figure 3.1). We analyzed small mammal mark-recapture data using robust design community-based N-mixture models (DRY models; [56]). We grouped similar species (*i.e.*, mice, chipmunks, woodrats, voles, and ground squirrels; see table B2) to resolve the issue of low capture rates for some. We compared models with null and group-specific detection and abundance, as well as abundance models with all combinations of elevation and percent forest cover. We used DIC to select a top model and estimate annual, group-specific detection and abundance in response to elevation and percent forest cover. We derived group-specific density for the sampling grid area (4900-m^2), scaled density to a 30-m pixel (900-m^2), and extrapolated group density to the remainder of the study area based on the predictions from our top model. We then converted density to total small mammal biomass per 900-m^2 by multiplying the group-specific mean mass by the estimated group-specific density of each 30m pixel and summing the totals for each group. Given the very small number of candidate models in the lagomorph and small mammal model sets, we evaluated variable importance based on whether coefficient credible intervals overlapped zero.

We assessed second order selection in parturient deer during the eight weeks post-parturition, a period during which fawns are most susceptible to coyote predation [44]. We confirmed date of birth either visually using hoof growth [57] or based on site fidelity (rASF) and movement using GPS data (BCPA; [58]) during the parturition period (late May through early July). We generated home ranges using kernel density (80% isopleth)

with an h-reference bandwidth estimator (R package *adehabitatHR*; [59]) for each parturient deer. We systematically sampled home ranges and the study area at 30-m, and compared the composition of the home range (1) to that of the study area (0) using hierarchical logistic regression. We incorporated a random effect of year to account for inter-annual variation in selection.

Finally, we quantified coyote resource selection during the summer using a step selection function [60]. We sampled local availability by randomly sampling from an individual's season-specific distribution for movement rate and turning angle. We conditioned used points on local availability (25 points per used point) and assessed selection using hierarchical conditional logistic regression with crossed random effects of individual and year. We incorporated fixed effects of cougar relative probability of use, relative probability of cougar carrion, lagomorph density, small mammal biomass, parturient deer relative probability of use, and distance to roads. We also included the behavioral state of individual coyotes (active vs. inactive), determined using 2-D accelerometer data and BCPA.

3. Results

(a) Cougar resource selection

Cougars in our study area exhibited strong crepuscular activity patterns, with peak activity patterns within two and a half hours before and after sunrise and sunset. Active cougars generally selected tree cover, with the strongest selection for conifer and aspen, at the third-order scale (tables 3.1 and B3). Cougars also weakly selected rocky/barren cover, which is often associated with canyons and intermediate-to-high ruggedness.

Active cougars generally avoided tertiary roads and open spaces (*i.e.*, grasslands), but remained at intermediate distances to both.

(b) Cougar kill locations

Cougars killed and cached prey in moderate-to-high ruggedness at intermediate elevation and in proximity to tree cover (>50%). These patterns are largely a reflection of where cougars and deer occur with a high probability, with one notable exception (tables 3.1 and B4). Active cougars appeared indifferent to springs, while deer preferred intermediate distances. However, kills had the highest probability of occurring in proximity to springs.

(c) Lagomorphs and other small mammals

We detected three species of lagomorphs on our spotlight transects: black-tailed jackrabbit (*Lepus californicus*), mountain cottontail (*Sylvilagus nuttallii*), and snowshoe hare (*L. americanus*). The distance sampling models indicated that lagomorphs, when grouped together, declined with elevation and percent forest cover (table B5). When estimated across the study area, lagomorphs exhibited exponential growth over the four years we surveyed (figure B1a). In addition, we detected 14 species of small mammals (table B2). We tested Poisson, zero-inflated Poisson, and negative binomial errors in our community N-mixture models [56]. However, only the negative binomial (NB) models produced robust posterior predictive checks (figure B2) and therefore limit our discussion to the NB results. Our NB models predicted the highest densities of small mammals at intermediate elevations, with species-specific responses to forest cover (table B6) and annual fluctuations in biomass largely a consequence of a volatile deer mouse

(*Peromyscus maniculatus*) population (figure B1b).

(d) Deer fawn site selection

Parturient deer selected for sites in proximity to tree cover (*i.e.*, Conifer, other hardwood, and Aspen in order of selection strength), while avoiding open areas (*i.e.*, grasslands). In addition, they selected for proximity to roads, intermediate ruggedness, moderate-to-high NDVI, and intermediate distances to springs (tables 3.1 and B7).

(e) Coyote resource selection

We identified three behavioral states using BCPA and k-means clustering, two distinctly active states and one inactive state. For the purposes of this analysis, we grouped the two active states in order to contrast the differences in resource selection between active and inactive coyotes. We considered coyote resource selection by incorporating factors associated with risk (e.g., distance to tertiary roads and cougar resource selection) and prey (e.g., cougar carrion subsidies, lagomorph density, small mammal biomass, and parturient deer resource selection) in a SSF framework (table 3.2). In general, coyotes strongly avoided tertiary roads and areas that had a high probability of use by cougars, particularly when inactive (figures 3.2a and 3.2b). However, coyotes selected areas with moderate probabilities of cached cougar kills, while avoiding areas with the highest probabilities (figure 3.2c), with a slight increase in use of such sites while active. In addition, coyotes strongly selected moderate-to-high lagomorph densities (figure 3.2d) and less so moderate small mammal biomass (figure 3.2e). However, coyotes did not appear to respond to areas favored by parturient deer (figure 3.2f). We further assessed individual variation in coyote response to deer fawning sites by

regressing lagomorph density at the coyote home range level with individual estimates for parturient deer site selection. We identified moderate individual variation with a trend indicating reduced selection for deer fawning sites as lagomorph densities increase (p = 0.044*;* figure 3.3).

4. Discussion

We implemented a community-based resource selection model to elucidate resource selection motivations for observed patterns of space use in a mesopredator, the coyote. Coyotes strongly selected areas with abundant small prey, particularly lagomorphs, while avoiding areas with a high probability of encountering cougars. Our spatial predictions match diet studies in coyotes, with prey composition largely fluctuating in response to lagomorph abundance [16,61]. Interestingly, our marginal estimates indicated coyotes are generally indifferent to areas favored by pregnant deer or deer with fawns, suggesting coyote predation on ungulate prey may be opportunistic within this system. Although we recognize that this pattern reflects distinct differences in prey-associated cover classes, the opportunistic and generalist tendencies of coyotes hint at an underlying community interaction as a driver of the observed heterogeneity in resource selection.

One plausible explanation is that competitor interference alters the landscape of risk and accessibility to some prey species. For example, Vanak *et al.* [62] demonstrated subordinate predators had restricted access to shared prey species as a consequence of apex predator presence and exhibited a range of risk averse behaviors, from fine-scaled avoidance to spatial partitioning. Our results support this explanation by indicating that

coyotes strongly avoided areas favored by the more dominant competitor. We demonstrate that although coyotes kill and consume mule deer fawns [41], it may be opportunistic and dependent upon the availability of alternative prey and the probability of encountering a dominant competitor. Competitor interference in the form of intraguild killing is common within this system, with eight of nine natural coyote mortalities attributed to cougars. Thus, as cougar resource selection largely coincided with our predictions for deer resource selection, spatial avoidance of cougars by coyotes to reduce the risk of intraguild killing may limit access to mule deer fawns. Similar spatial changes in foraging behavior were experimentally observed in response to perceived competitor interference by larger predators in stoats (*Mustela erminea*) [63]. Although cougars are prevalent throughout our system, evidence from studies in the eastern U.S. indicate that in the absence of a dominant competitor, coyotes will utilize forested landscapes favored by white-tailed deer (*Odocoileus virginianus*) and become the primary predator of adult deer and their fawns [64,65]. This supports the idea that coyotes may underutilize fawns as prey while avoiding cougars within this system and perhaps in other areas where top predators remain.

Changes in resource availability may alter a predator's response to risk associated with food acquisition. For example, coyotes may favor smaller prey over more dangerous ungulates when safer prey are abundant due to the significant risk of injury or death during encounters with dangerous prey [66]. Our results show that coyotes are increasingly likely to select areas with a higher probability of encountering parturient deer as lagomorph densities decline at the home range level and may reflect density-dependent prey switching in coyotes. Experimental studies of some predators have

demonstrated that hunger can provide motivation for riskier behavior with consequences for the way they use space [67]. In other cases, mesopredators may prioritize resource acquisition while balancing risk of encountering apex predators through fine-scale spatiotemporal avoidance [68].

In our study, risk could have included increased prey handling danger, elevated probability of encountering cougars, or both. When lagomorphs were less abundant, coyotes may have been more willing to risk encountering cougars while searching for fawns, with the strength of selection for deer fawning sites mediated by cougar-related mortality. Yet, coyotes appeared to select sites with higher probabilities of encountering cougar caches, suggesting coyotes may be adept at balancing risk with access to carrion even in times of abundant food. In similar systems where wolves and coyotes co-occur, wolf-killed scavenging opportunities are important to coyotes [42,69].

Although we provide compelling evidence for the role of prey availability in coyote resource selection patterns, we want to underscore the role individual variation has on resource selection, particularly in a generalist predator. Resource selection analyses are often performed in a mixed modeling framework [54] in an effort to account for unmeasured variation associated with individuals or blocks of time (e.g., year), as we do here. However, some of the variation we attribute to individuals is a consequence of violating the assumption that selection is constant at all levels of resource availability, or in the case of time, that resource availability is static rather than dynamic. If resources are improperly quantified, or misrepresented as available, resource selection analyses can lead to biased expectations of animal space use [48]. Thus, common use of resource indices as measures of habitat may lead to a biased understanding of the resource needs

for a given species and inflate our expectations of variation in individual behavior and time. Although we included some resource indices in our analysis, we estimated all factors that we hypothesized would strongly influence coyote resource selection (e.g., competitor encounter probabilities, as well as prey density and biomass) dynamically over time. This permits a more direct measure of what coyotes were responding to on the landscape. Studies of community processes and predator guild dynamics using data from camera trapping have demonstrated the importance of spatial components of risk and prey resources in shaping predator co-occurrence at coarser scales [18]. Although our efforts do not eliminate the need for considering individual random effects, we suggest that investigating resource selection in the context of community dynamics, where interactions among multiple species are considered, is a more powerful approach for distinguishing variation in intrinsic selection behavior of individuals from differences in selection that are due to varying resources available to individuals. Thus, we encourage use of dynamic community-integrated resource models (e.g., [70]), particularly in multi-predator-prey systems to enhance our general understanding of the motivations surrounding animal resource selection and space use.

We provide novel information pertaining to the influence of prey resources and competitor risk on space use in a mesopredator that has relevance beyond the scope of our study system. The influence of cougars on resource selection patterns and movement decisions of coyotes we documented lends further support for the mesopredator release hypothesis (MRH, [20]). Although we did not explicitly test MRH, the mediating effect of cougars may limit the impact of coyote predation on mule deer fawns. However, in the absence of a more dominant competitor, a mesopredator, such as the coyote in the eastern

U.S., serves as the apex predator and can potentially limit prey, such as white-tailed deer (*Odocoileus virginianus*), through the direct and indirect effects of predation [71]. Further, our findings support the role of trophic complexity in maintaining community diversity and could have important implications for the way we manage and conserve some prey species [19,72]. Our study demonstrates the need for considering multiple species in evaluations of mesopredator resource selection given the role of competitor interactions in shaping communities. More generally, it provides a format to evaluate mesopredators from any system where spatial partitioning is likely to occur within a competitively asymmetric guild of predators.

5. Ethics

Animal capture and handling protocols were approved by USDA-WS National Wildlife Research Center (IACUC: QA-1907) and Utah State University (IACUC-2182).

6. Data accessibility

We will make animal location data and prey survey data available upon publication.

7. Funding

This research was supported by the Utah Division of Wildlife Resources (Coyote grant #121560), USDA-Wildlife Services - National Wildlife Research Center, NASA Biodiversity and Ecological Forecasting Program (Climate and Biological Responses, grant no. NNH10ZDA001N), Ecology Center and Department of Wildland Resources at Utah State University, and Utah's Hogle Zoo.

8. Authors' Contributions

PJM and JKY conceived the study. PJM lead the writing and conducted the analysis. PJM and JKY collected predator, lagomorph, and small mammal data. JKY and DS revised the manuscript. DS collected deer data.

9. Competing interests

We declare no competing interest.

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11. Tables and Figures

Table 3.1. Coefficient estimates for all fixed and random effects in the cougar (3rd order), cougar cache (2nd order), and parturient deer (2nd order) resource selection models. All continuous metrics are centered and scaled by one standard deviation. CI – 95% posterior credible intervals. *Reference category is all other aspects not specified.

	Cougar Resource selection (Active)				Cougar Cache Sites				Parturient Deer Resource selection			
Fixed Effects	**mean**	**SD**	**Lower CI**	**Upper CI**	**mean**	**SD**	**Lower CI**	**Upper CI**	**mean**	**SD**	**Lower CI**	**Upper CI**
Dist. to Aspen	-0.387	0.074	-0.533	-0.245					-0.102	0.028	-0.156	-0.047
Dist. to Aspen^2	0.097	0.032	0.033	0.16					-0.054	0.020	-0.094	-0.014
Dist. to Barren	-0.018	0.033	-0.082	0.048								
	-0.041	0.016	-0.072	-0.011								
Dist. to Conifer	-0.613	0.059	-0.729	-0.498					-0.560	0.033	-0.625	-0.496
	-0.072	0.051	-0.177	0.023								
Dist. to Grass	0.186	0.04	0.108	0.263					0.471	0.017	0.439	0.504
Dist. to Grass^2	-0.191	0.027	-0.244	-0.139					-0.130	0.009	-0.148	-0.114
Dist. to HW	-0.322	0.049	-0.419	-0.227					-0.360	0.020	-0.401	-0.320
Dist. to HW^2	0.122	0.017	0.089	0.155					-0.078	0.016	-0.110	-0.047
Dist. to PJ	-0.161	0.061	-0.283	-0.039					0.730	0.025	0.680	0.779
Dist. to PJ^2	0.024	0.021	-0.018	0.066					-0.262	0.009	-0.279	-0.244
Dist. to Roads	0.113	0.038	0.04	0.185	0.377	0.044	0.292	0.463	-0.258	0.014	-0.286	-0.230
Dist. to Roads^2	-0.065	0.018	-0.101	-0.031	-0.186	0.022	-0.23	-0.144	0.043	0.004	0.035	0.051
Dist. to Shrub									-0.050	0.018	-0.084	-0.014
Dist. to Shrub^2									-0.013	0.005	-0.023	-0.003
Dist. to Tree Cover (>50%)					-1.526	0.103	-1.737	-1.343				
Dist. to Tree Cover^2 (>50%)					0.369	0.102	0.152	0.544				
Dist. to Springs	0.041	0.028	-0.013	0.094	-0.613	0.084	-0.781	-0.449	0.575	0.015	0.545	0.604
Dist. to Springs^2	-0.065	0.02	-0.104	-0.026	-0.388	0.074	-0.532	-0.241	-0.270	0.013	-0.297	-0.244
Max NDVI									1.056	0.026	1.005	1.108
Max NDVI^2									-1.099	0.021	-1.140	-1.058
Ruggedness, TRI												
Ruggedness, TRI^2												
Elevation					1.089	0.114	0.88	1.316				
Elevation^2					-1.131	0.067	-1.266	-1.008				
Ruggedness, VRM	0.08	0.028	0.026	0.138	0.143	0.048	0.051	0.24	0.078	0.012	0.054	0.102
Ruggedness, VRM^2	-0.048	0.02	-0.09	-0.008	-0.11	0.044	-0.196	-0.028	-0.035	0.011	-0.056	-0.014
Slope					0.381	0.054	0.275	0.484				
Slope^2					-0.316	0.032	-0.381	-0.254				
East*					0.25	0.065	0.12	0.372	0.357	0.027	0.305	0.409

Table 3.1 cont.

South*					0.115	0.069	-0.019	0.25	0.056	0.030	-0.002	0.115
West*	-0.302	0.066	-0.433	-0.176	-0.865	0.096	-1.048	-0.68	-0.377	0.028	-0.432	-0.323
No Aspect*					0.704	0.802	-1.095	2.042	-0.451	0.102	-0.653	-0.258
Random Effects												
(RE) Year sd	1.213	0.701	0.402	2.817	1.546	0.727	0.719	3.519	1.647	0.951	0.696	4.257
(RE) Year mean	-1.18	6.978	-14.876	12.224	-5.679	0.761	-7.217	-4.085	-1.480	0.956	-3.508	0.546
(RE) Individual sd	0.508	0.219	0.246	1.072								
(RE) Individual mean	-0.987	6.973	-14.556	12.667								

Table 3.2. Selection coefficients derived from a step-selection function analysis of coyote movement during active and inactive behavioral states. Lower and upper CI are corresponding 95% posterior credible interval limits.

	Active				**Inactive**			
Selection Coefficient	**mean**	**SD**	**Lower CI**	**Upper CI**	**mean**	**SD**	**Lower CI**	**Upper CI**
Dist. to tertiary roads	-0.100	0.023	-0.143	-0.054	0.133	0.031	0.073	0.197
Dist. to tertiary roads^2	-	-	-	-	-0.079	0.014	-0.107	-0.053
Probability of use by cougars	-0.249	0.030	-0.307	-0.191	-0.331	0.033	-0.396	-0.267
Probability of cougar cache	0.219	0.040	0.139	0.297	0.311	0.044	0.226	0.394
Probability of cougar cache^2	-0.054	0.014	-0.083	-0.027	-0.091	0.016	-0.121	-0.062
Probability of use by deer	-0.056	0.028	-0.112	-0.006	-0.058	0.031	-0.116	0.003
Lagomorph density	0.308	0.060	0.189	0.425	0.241	0.058	0.121	0.356
Lagomorph density^2	-0.056	0.030	-0.116	0.000	-0.050	0.029	-0.107	0.005
Small mammal biomass	0.249	0.052	0.150	0.351	0.000	0.055	-0.107	0.106
Small mammal biomass^2	-0.176	0.029	-0.234	-0.120	-0.094	0.031	-0.153	-0.033

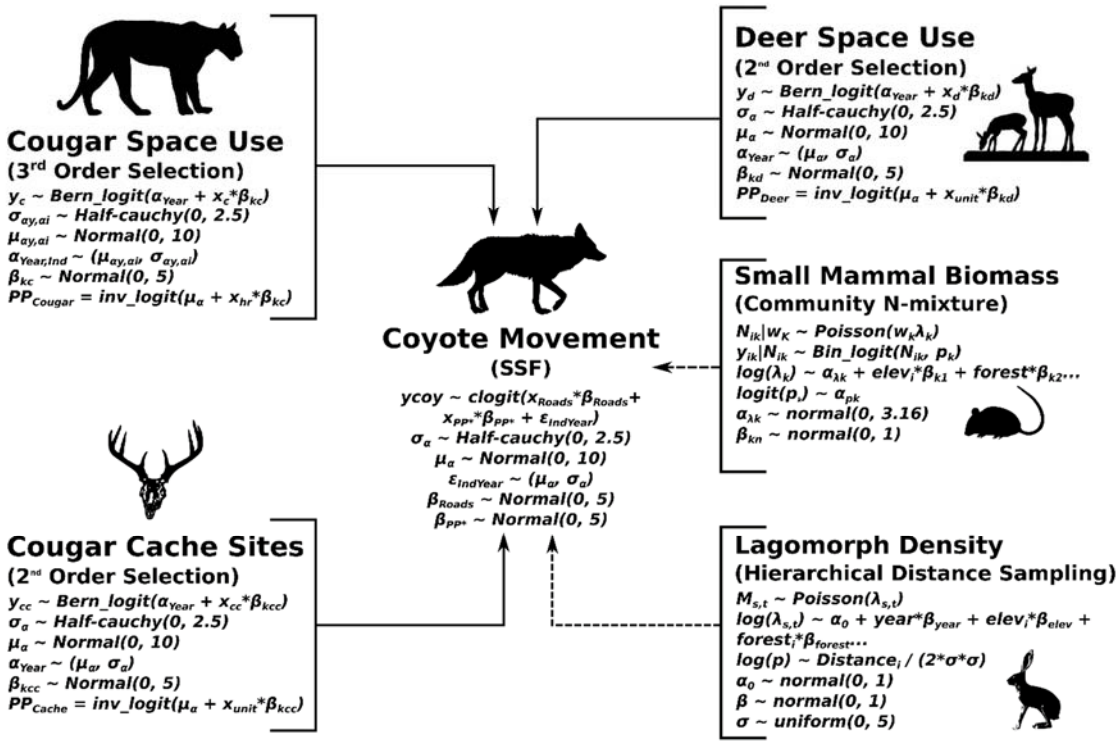

Figure 3.1. A conceptual model depicting how sub-models are interconnected, along detailed sub-model specifications highlighting the data model, parameters, hyper-parameters, and associated priors. We estimated sub-models with solid lines and the overall coyote step-selection model concurrently, which accounted for uncertainty in the associated sub-models. We used mean estimates derived independently from the sub-models with dashed lines.

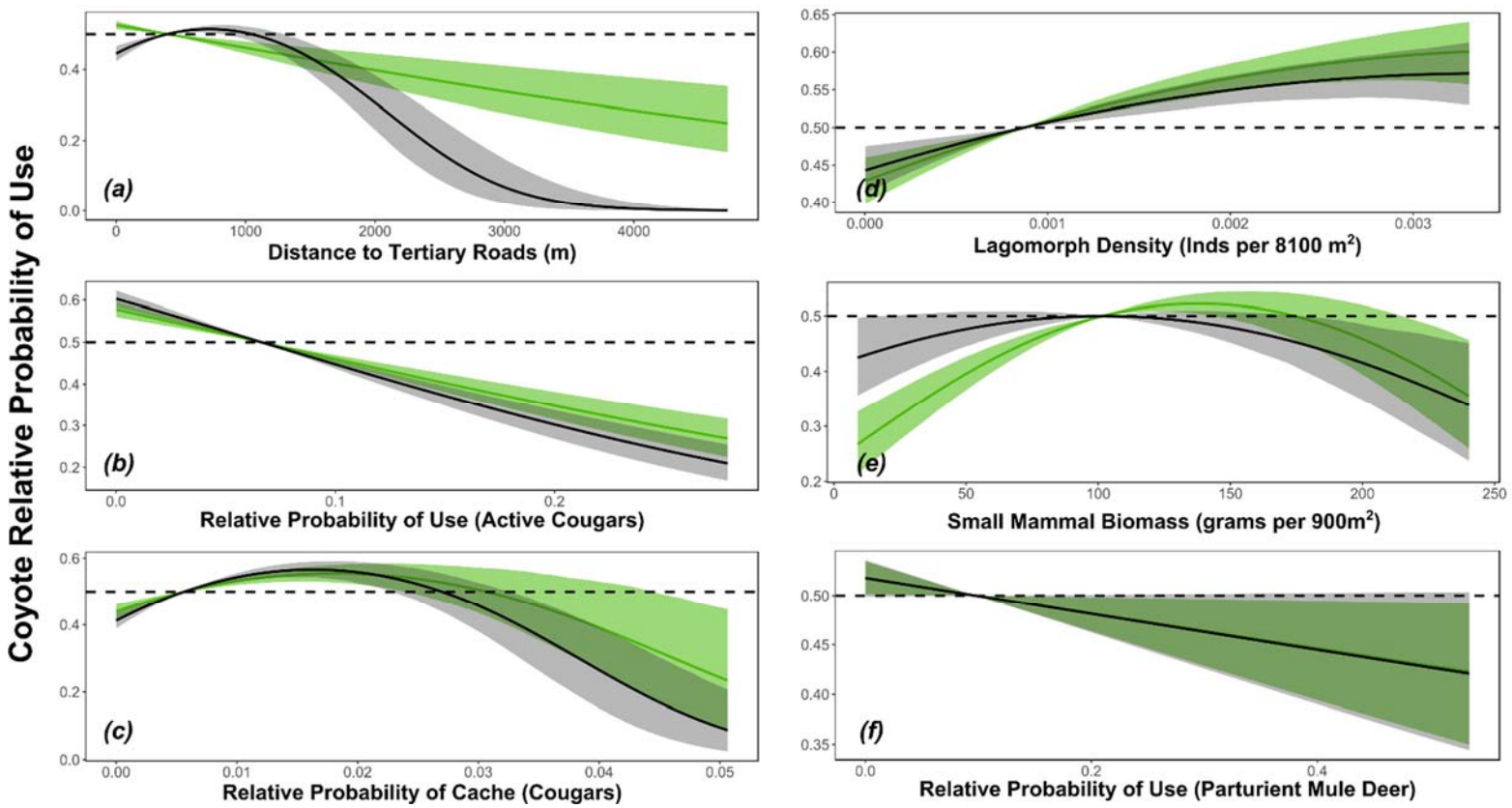

Figure 3.2. The marginal (*i.e.*, population-level) estimates for the relative probability of use by coyotes as predicted across the observed ranges of the six covariates: distance to tertiary roads (a), cougar probability of use (b), probability of cougar cache (c), lagomorph density (d), small mammal biomass (e), and parturient deer probability of use (f). Color ribbons depict the 95% credible intervals for active (green) and inactive (grey) coyotes.

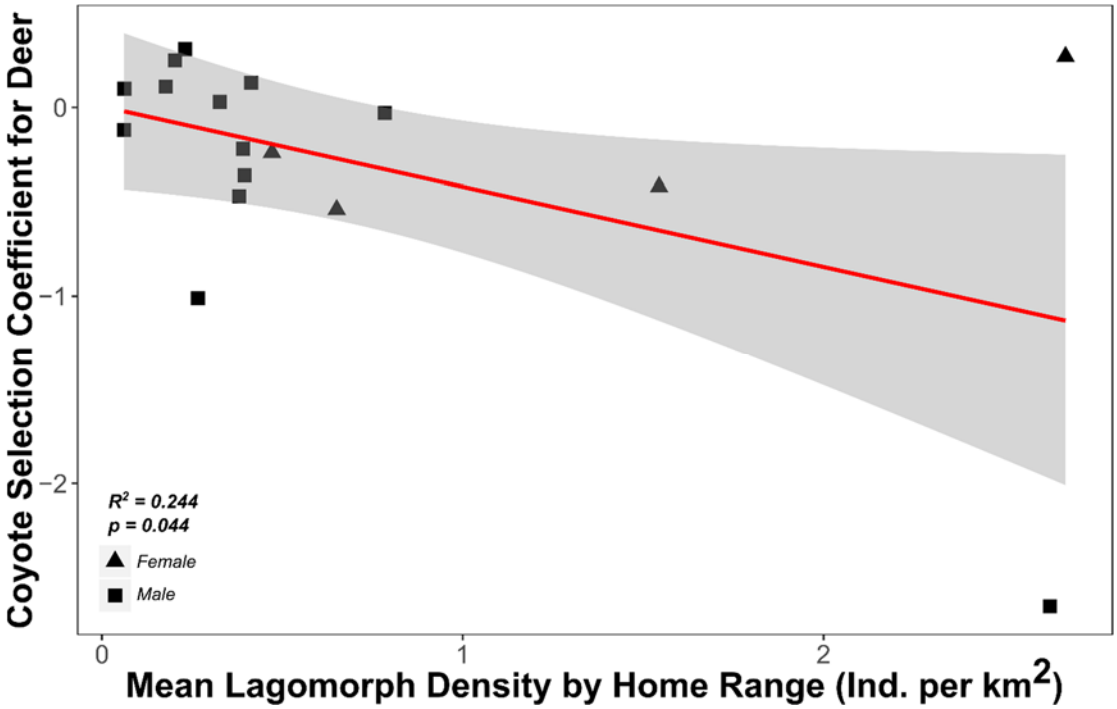

Figure 3.3. The functional relationship between lagomorph density at the individual coyote home range level relative to selection for higher probability of use sites in parturient deer. Positive and negative coefficients indicate selection and avoidance, respectively. Note that the one outlier female (triangle) at high lagomorph densities had dependent young at the time. The grey ribbon is the 95% confidence interval and Ind. per km^2 is the number of individuals per square kilometer.

CHAPTER 4

SPACE USE OF AN APEX PREDATOR IN RESPONSE TO SEASONAL MOVEMENTS OF PREY AND ANTHROPOGENIC RISK: COUGAR AS A MODEL SYSTEM[3]

SUMMARY

Apex predators promote species coexistence and sustain community diversity. They are also disproportionately impacted by anthropogenic activities, owing in part to their large spatial requirements and slower reproductive life histories, which can in turn lead to local extirpation or extinction. Thus, apex predators must be able to exhibit sufficient behavioral plasticity to respond to changes in landscapes and sources of anthropogenic pressure while maximizing access to prey resources. An effective approach to evaluating behavioral responses to anthropogenic disturbance is through the use of resource selection models which can account for the changes in the availability of anthropogenic landscape change that is relevant to the predator in question. However, such changes must also account for patterns of prey space use to separate anthropogenic effects from prey responses. Here, we used step-selection functions to evaluate predator space use and resource selection in response to anthropogenic activity at two scales, the population and individual level, while accounting for space use in primary prey. We specifically evaluated concurrent movement and resource selection in cougars (*Puma concolor*), mule deer (*Odocoileus hemionus)*, and Rocky Mountain elk (*Cervus elaphus*

[3] Mahoney, P.J., D. Stoner, and J.K. Young. *Ecology*.

nelsoni) using step-selection functions. We tested for differences in cougar resource selection between harvest and non-harvest seasons at the population level, as well as functional responses in selection by individual cougars to the mean distance to roads within home ranges during the harvest season. We found that cougars avoided proximity to roads regardless of season. In addition, cougars selected for more rugged terrain than prey and when active, moved into smoother terrain presumably to access prey. The strength of selection for rugged terrain increased during the cougar harvest season, potentially in response to increased anthropogenic pressure. However, we were unable to identify an individual functional response between selection for rugged terrain and mean distance to roads, indicating individual cougars may not respond differentially to variation in road access during the harvest season. Our findings provide improved clarity of anthropogenic impacts on space use in apex predators, while highlighting the importance of considering simultaneous space use of their prey.

INTRODUCTION

The impacts of urbanization and increased human access to wildlands are manifold with implications at all ecosystem levels. Humans represent a significant source of risk and mortality to most terrestrial and marine species (Worm and Paine 2016). Examples of such anthropogenic impacts abound worldwide, with subtler effects on animal behavior (*e.g.*, Halfwerk and Slabbekoorn 2015) to larger effects resulting in local extirpation or extinction (*e.g.,* Ceballos et al. 2015, McCauley et al. 2015). Anthropogenic activity and related causes of wildlife mortality disproportionately impact species at the highest trophic levels with added costs for other community members as a

result of altered trophic dynamics (Prugh et al. 2009, Estes et al. 2011). This may in turn upset predator-prey processes (e.g., increased refugia, Berger 2007) and contribute to the inevitable trophic downgrading of some communities (Estes et al. 2011).

Predators can preserve community diversity by promoting coexistence among competitors at lower trophic levels while indirectly reducing the impacts of first order consumers on primary producers. Apex predators are important to ecosystems worldwide (Estes et al. 2011), yet they are regularly subjected to anthropogenic population control measures in an effort to mitigate conflict with humans over livestock or wild game (Conover and Roberts 2016). In addition, the relatively large spatial requirements and slower reproductive life-histories of large predators can increase the susceptibility of populations to the potentially destabilizing effects of anthropogenic activity and landscape change (Cardillo et al. 2005). To persist, apex predators must be able to exhibit sufficient behavioral plasticity to respond to changes in landscapes and sources of anthropogenic pressure while maximizing access to prey resources. Remarkably, many large carnivores can persist in human-dominated landscapes provided sufficient time to adapt to changes in the absence of strong population control, particularly with sufficiently large population sizes to maintain genetic diversity (Benson et al. 2016).

To better understand how carnivores respond to anthropogenic activity, ecologists often investigate all hypothesized factors that influence individual movement and space use within a resource selection framework (e.g., resource selection functions, RSF; (Manly et al. 2007). Resource selection analyses (RSA) attempt to derive an empirical depiction of species' habitat by quantifying features of the landscape relevant to all behavioral components of life history (e.g., reproductive or foraging sites, hereafter

resources), including factors or behaviors beneficial in mitigating mortality risk (Hebblewhite et al. 2005). RSFs often compare feature-specific ratios of animal use to availability on the landscape. Although theory predicts that animal space use should be proportional to availability in key components of habitat (*e.g.*, Ideal Free Distribution Theory; Fretwell and Lucas 1969), this assumes selection is constant at all levels of resource availability. Yet, space is rarely homogeneous and the features that contribute to landscape diversity, as well as anthropogenic risk, are unlikely to be consistent across multiple spatial extents. Therefore, within or between individual variation in behavior may permit resource selection to vary with availability in both space and time (Bolnick et al. 2002). Similarly, strength of resource selection may respond to perceived changes in resource accessibility (though availability may be numerically constant) as shifts in conspecific, competitor, or predator densities occur (*e.g.*, Basille et al. 2015). Thus, the dynamic nature of availability related to specific components of an animal's habitat is integral to understanding how individuals respond behaviorally to changes in the environment.

Documenting changes in resource selection in response to shifts in availability, or functional responses to resource availability (Mysterud and Ims 1998), can be an effective strategy for identifying behavioral responses to and tolerance for anthropogenic disturbance. In the most extreme case, where landscapes become increasingly risky as a result of human activity, strong selective pressures act on animals to alter their behavior such that resource selection may vary across a gradient of risk. For example, Benson et al. (2015) demonstrated canids (*Canis* spp.) that could modify their behavior by avoiding roads more so during daylight in areas of higher road density experienced reduced

mortality risk. Similarly, Kojola et al. (2016) showed that gray wolves (*C. lupus*) became increasingly nocturnal during yard visitations in areas with higher densities of human residences, and that sub-adults visited more frequently than adults. Johnson et al. (2015) showed that black bears (*Ursus americanus*) were more likely to use developed areas, and the associated caloric subsidies, during periods when natural foods were scarce. Knopff et al. (2014) demonstrated that cougars (*Puma concolor*) were more likely to use anthropogenic features at night, while wildland cougars more strongly avoided said features than their extra-urban counterparts. Yet, in order to capture the influence of anthropogenic risk on predator space use, one must also quantify potentially confounding factors which may also contribute to the observed changes in predator space use behavior. Often in predator-prey systems, changes in prey availability can be responsible for observed shifts in predator space use (Hofer and East 1993, Hammond et al. 2007). Kitchen et al. (2000) demonstrated that despite no changes in prey availability, coyotes exhibited more nocturnal activity patterns in areas with extensive anthropogenic harvest pressure. However, a meta-analysis of wolf studies suggested increased nocturnal activity of wolves correlates to diet and road density while reduced diurnal activity relates to the potential presence of humans (Theuerkauf 2009). Thus, to document individual functional responses in a predator, a community-based resource selection approach is necessary to identify behavioral changes that are independent of shifts in prey space use.

Identifying functional responses to changes in resource availability is key to improving our general understanding of animal space use, while permitting more informed predictions in changing environments (i.e., landscape and/or climate change; Street et al. 2015). In addition, empirical investigations of hypothetical functional

responses will provide a necessary next step towards linking fitness with space use (Leclerc et al. 2015, Losier et al. 2015, Street et al. 2016). The objective of this study was to identify changes in predator resource selection in response to anthropogenic activity at two scales, the population and individual level, while accounting for space use in their primary prey. To meet this objective, we investigated cougars as a model apex predator in a system with extensive, seasonally dependent harvest pressure. Within our study system, the primary hunting strategy involves the use of hunting hounds from early winter through mid-spring and hunter harvest represents the primary source of cougar mortality and thus, represents a significant source of risk. Yet, variation in human access, in addition to experience gained while evading hounds on failed hunts, provides individual cougars with opportunities to respond to changes in seasonal risk and increases in human harvest pressure. In an effort to separate prey response from anthropogenic risk response, we also include dynamic space use in two seasonally migrant prey species (Rocky Mountain elk: *Cervus elaphus nelsoni*; mule deer: *Odocoileus hemionus*), that together consist of over 90% of the cougar diet in this region (Table C1).

MATERIALS AND METHODS

Study area

We monitored cougar, elk, and mule deer space use in a 1,500-km^2 area of Fishlake National Forest, Utah. The study system is highly heterogeneous and characterized by a diverse array of elevation-dependent cover types that reflect differences in seasonal moisture regimes. The elevation ranges from 1430 to 3400 meters with lower elevations dominated by shrublands (*Artemisia spp.* and *Chrysothamnus spp.*),

mid-elevations by pinyon (*Pinus edulis*), juniper (*Juniperus osteosperma*), gambel oak (*Quercus gambelii*), and mahogany (*Cercocarpus ledifolius and C. montanus*), and higher elevations by alpine meadows (*Achnatherum spp.*), sagebrush (*A. tridentata*), aspen (*Populus tremuloides*), and conifer (*Abies lasiocarpa, Pseudotsuga menziesii,* and *P. ponderosa*). Precipitation on Monroe Mountain primarily arrives in the form of snow from mid-to-late winter, with often highly variable spring mixed precipitation, late summer monsoonal rains, and dry falls.

Animal monitoring and analysis

From 2011 through 2015, we deployed programmable global positioning system (GPS) collars on 11 cougars (2 males and 9 females; animal years = 26), 26 elk (26 cows; animal years = 77), and 17 deer (17 does; animal years = 39) in Fishlake National Forest, Utah. Cougars were treed using trained hounds and immobilized for processing using a Ketamine/Xylazine cocktail. Elk and deer were captured using state-contracted helicopter capture crews during the winter and spring of each year.

Mule deer and elk comprised over 90% of a cougar's diet (Table C1) and thus, cougar movement is expected to shift in response to changes in prey spatial distributions. Both ungulates exhibit a diversity of migration patterns within this system, in some cases moving long distances between neighboring mountain ranges while others travel only short distances in response to local changes in climate and food availability. However, both generally migrate along an elevation gradient, with movement towards lower elevations initiated in the fall following abrupt changes in climate and towards higher elevations in the spring following warming trends and vegetative green-up (Monteith et

al. 2011, Merkle et al. 2016).

In order to represent these seasonal influences on movement and resource selection, particularly in the context of a dynamic predator-prey system, it is necessary to consider a framework that accounts for both simultaneously. Thus, we employ step-selection functions (SSF; Fortin et al. 2005, Thurfjell et al. 2014), where used points are conditioned on 'local' availability, which were in turn characterized by 50 random draws from distributions characterized by an individual's movement rate (*i.e.*, distance in meters / location fix interval) and turning angle. We further partitioned individuals into distinct movement 'bursts' in cases where missed fix intervals contributed to gaps greater than 72 hours. As we took a predator-centric view with the intent of documenting where prey had the highest probability of occurrence, we divided the elk and deer datasets into monthly intervals and estimated individual movement distributions and resource selection accordingly.

After developing models of ungulate movement and resource use, we directly estimated the monthly relative probability of use by each ungulate species based on used and available spatial covariates in the cougar SSF. We used conditional logistic regression at all levels of the model while including all metrics at the finest temporal resolution possible (*e.g.,* ungulate-specific monthly probability of use for cougar models, NDVI daily or 7-day for ungulate models). Doing so permitted us to investigate a potential response in cougar movement and resource selection to human activity while accounting for concurrent space use in the two primary prey species within this system. We built all models in R (v3.3.2, R Core Team 2016) using the *coxph* function from the *survival* package (v2.38-3; Therneau 2015). We estimated robust standard errors using

sandwich estimators by clustering individuals to account for lack of independence within individual samples. Although mixed conditional logistic regression is encouraged for SSF (Duchesne et al. 2010), as with mixed survival regression, misspecification of random distributions in a time-to-event context can lead to biased coefficients (Hosmer et al. 2008). Thus, albeit less flexible, the clustering function in R's conditional logistic model permits a conservative means of estimating robust standard errors in cases where simple grouping structure exists while reducing risk of bias associated with model misspecification (Duchateau and Janssen 2007).

Spatial data

We collected data for several ecologically relevant spatial covariates for use in our SSF models, each of which was hypothesized to influence species-specific movement and resource selection. We incorporated distance to tertiary roads (*i.e.*, unpaved roads) as an index of human access. We used a distance to road metric as it best captures avoidance of linear features in a SSF framework (Thurfjell et al. 2014). We did not include distance to primary and secondary roads (i.e., paved roads and highways) as these were almost entirely captured by the margins of the study system, and therefore confounded by elevation and potentially area edge effects. In addition, we included distance to point and linear water features given the relevance for large mammals in semi-arid systems. We estimated elevation, vector ruggedness metric (VRM; Sappington et al. 2007), and categorical aspect (*i.e.*, North, East, South, West, and No Aspect) from a 30-m USGS digital elevation maps (DEM, Utah Mapping Portal, 2015). North represented the reference category due to differences in cover classes and snow pack, except in cases

where excluded levels of aspect were combined with North as the reference. We derived landcover from LANDFIRE (LANDFIRE 2012) and simplified cover classes into aspen, other hardwood (*e.g., Quercus* spp. and *Cercocarpus* spp.), shrublands, grasslands, pinyon or juniper, other conifer, mixed hardwood and conifer, and rocky/barren. We then estimated distance to the nearest pixel for each landcover class at a 30-meter resolution. We used daily (2011 – 2014) or 7-day (2015) normalized vegetation index (NDVI) as an index of forage at a 500-meter resolution (Pettorelli et al. 2011, Stoner et al. 2016). We assessed all continuous metrics for problematic correlations using a combination of Pearson's R ($R < 0.70$) and variance inflation ($VIF < 4$) by means of the R package *usdm* (Naimi 2015). We standardized (*i.e.*, centered by means and scaled by one standard deviation) all continuous metrics to improve model convergence.

Model selection and validation

We considered all possible combinations of spatial covariates, including second-order polynomials for continuous metrics and diurnal interactions with relevant spatial covariates pertaining to risk (*e.g.*, distance to tree cover, distance to roads, or elevation/ruggedness), for both prey species independent of the overall cougar analysis. For the cougar model, we included spatial covariates as well as the relative probability of use by the respective prey species, which were estimated independently on a monthly basis. In addition, we included a metric for harvest season as cougars are managed as a game species by the Utah Division of Wildlife Resources (UDWR 2015). We monitored cougars on the Monroe management unit (23A), a unit that opens for limited entry (*i.e.*, lottery based) cougar season during the second week in November (11th through 14th)

through the last week in February (26th or 27th), with an extended quota season through the end of May (30th or 31st). Thus, we included a binary covariate reflecting whether location occurred within (1) or outside (0) of the respective annual cougar pursuit/harvest season.

We ranked models by quasi-likelihood under independence criterion (QIC; Pan 2001) and selected the most parsimonious nested model from the top candidate models (ΔQIC < 4) for estimating the relative probability of use in both prey species during each month of the year. We did not model average as we included interactions that ultimately changed the interpretation of main effects such that model averaging was no longer meaningful. We validated the top species' models using 5-fold cross validation for conditional logistic regression (Daniel et al. 2009) using the R package *hab* (Basille 2015). In addition, we evaluated the influence of our random availability sampling on our representation of availability within each sub-model (Northrup et al. 2013, Paton and Matthiopoulos 2016) by visualizing spatial data at incrementally smaller sample sizes. We retained the smallest sample that was representative of our largest sample (*i.e.*, 50 random points) at the individual level.

Functional responses

We evaluated functional responses to changes in availability at two scales. First, we identified changes in resource selection as a function of changes in the landscape of risk by incorporating interactions between harvest and non-harvest seasons and distance to roads in the SSFs. These indices included distance to roads and ruggedness. Second, we generated individual-level selection coefficients for distance to roads and ruggedness,

during active and inactive periods, and tested for a relationship between selection coefficients and the availability of human access during the harvest season at the home range level using linear regression.

RESULTS

Deer and elk

We removed distance to mixed forests (*i.e.*, aspen and conifer) and distance to agriculture due to correlations with other forest cover types and elevation. Aspen, conifer, and hardwood cover types were all strongly collinear with elevation as well. However, we included elevation in a subset of models independent of the higher elevation forest types as a more parsimonious alternative. The two ungulate species exhibited seasonal and thus monthly differences in movement and resource selection (Tables C2-C5). Population level patterns in both species demonstrate seasonality associated with elevation or elevation-dependent cover types (Fig. 4.1). During the late spring and summer months, both species selected for proximity to aspen. Elk avoided proximity to conifer stands, although deer neither selected nor avoided conifer. Elk also selected for grasslands. During the winter, both deer and elk generally selected for pinyon and juniper stands while deer also selected for shrublands, an indication that elk were more commonly at higher elevations during the colder months. Our models provided little support for higher probability of use in rugged areas during periods of higher human activity (*i.e.*, daytime). Instead, there was some support that during daylight hours, both species tended to avoid more open cover types (*e.g.*, shrub and grasslands) and selected for areas with tree cover. Both species generally avoided proximity to tertiary roads.

Cougars

In general, cougars selected for areas in proximity to tree cover and associated with moderate slopes and terrain ruggedness (Table 4.1 & C6). Cougars moved into less rugged terrain during crepuscular periods of activity, utilizing more rugged terrain during periods of inactivity. Cougars avoided tertiary roads, utilizing areas at intermediate distances to these linear features. Recall, that paved roads associated with townships made up the fringe of the study area and likely contributed to this non-linear effect of unpaved roads. In general, cougars selected for areas favored by mule deer over that of elk. However, during the cougar harvest season (*i.e.*, winter), cougars switched their selection for sites utilized by elk which may indicate seasonally dependent prey switching in this ungulate specialist (Table 4.2). Of 285 documented kills over the course of three years, 55.7% (SE=0.07) of elk were killed by cougars during the harvest season as opposed to 46.5% (SE=0.06) of mule deer. We dropped a season at the beginning and end of our work due to insufficient samples for this comparison. Similarly, elk composed 31.0% (SE=0.03) of cougar diets during the harvest season as opposed to only 23.7% (SE=0.04) during the non-harvest season.

Generally, cougars selected for more rugged terrain when inactive and would leave rugged areas during peak activity periods (±2.5 hours of sunrise/sunset) (Fig. 4.2), presumably to access prey. Our results demonstrate a shift in cougar space use towards more rugged terrain during the cougar harvest season relative to the non-harvest season, with almost double the effect size (Table 4.2 and Fig. 4.2). However, we were unable to identify an individual functional response in selection for rugged terrain as a function of

mean distance to roads at the home range level (Fig. 4.3).

DISCUSSION

We developed a series of movement and resource selection models for both predator and prey in an effort to disentangle a prey response from a potential response to anthropogenic activity. In doing so, this study improves our general understanding of predator space use. We generated monthly movement models to capture seasonal movements in migratory prey populations. We believe these monthly models accurately reflect our expectations of where elk and deer are likely to occur during these seasons but recognize that, if future studies used more fine-scale data, they could develop step-selection models by calendar day and behavioral state (*e.g.*, migratory vs. non-migratory states) and reduce some of the uncertainty regarding the location of prey. Even so, our models met our monthly expectations of space use in the respective prey populations, with both deer and elk exhibiting seasonal movements indicative of a vertical migration.

We demonstrated that cougars exhibited space use patterns that are somewhat independent of the relative probability of use by prey. Although cougars exhibited strong, seasonally dependent selection for areas used by deer and elk, once accounted for, our models indicated cougars selected for terrain that likely benefited their ambush strategy for prey capture. Cougars favored areas in proximity to tree cover, moderate slopes, and moderate ruggedness more so than predicted by prey space use alone. In addition, cougars strongly selected for areas used by mule deer during the non-harvest season (*i.e.,* spring through fall). This is unsurprising given mule deer comprise approximately two thirds of their diet, are more abundant in this system, and represent less risky prey for

solitary cougars due to their smaller body size (Knopff et al. 2010).

Interestingly, cougars exhibited a shift towards elk use areas during the cougar harvest season (*i.e.*, winter and early spring). This is likely a reflection of changes in prey accessibility as elk often favored higher elevations than deer during the winter months. Although not a strong shift, we documented a 7.3% increase in the occurrence of elk in the diet of cougars with over half of the elk kills occurring during the harvest season. These patterns in prey selection may suggest prey switching as an outcome of differences in seasonal space use by preferred prey or an increased susceptibility to predation in larger-bodied, riskier prey (*i.e.*, snow depth; Hebblewhite 2005). The strength of this switching may strongly depend upon the relative abundance of each prey species and the severity of climatic conditions during the respective seasons, which we do not have sufficient resolution to address here. Regardless, this raises an important question pertaining to whether this shift towards risky prey is an outcome of life-history strategy, historical competition with open-land predators (*e.g.,* wolves), or an outcome of human risk factors.

In general, our results support a possible population-level response in cougars to human activity. Regardless of season, cougars more strongly avoided proximity to tertiary roads than their prey, a trend observed in other mammalian carnivores (e.g., Benson et al. 2015). In addition, cougars selected for more rugged sites during periods of inactivity. However, the strength of this shift towards ruggedness increased during the cougar harvest season (Fig. 4.2), even after accounting for movements by prey. Unfortunately, we were unable to resolve functional responses by individual cougars to changes in human activity or risk. However, this is not to say that individual functional

responses to human activity are absent from this system or in cougars in general. Although incidental trapping of cougars does occur, most reported cougar harvest in Utah is via hound hunting. Hounds are tremendously effective at trailing cougars over long distances and represent the primary source of risk for harvested populations in Utah (Stoner et al. 2006, 2013). Thus, if we expect to see a functional response to human activity at the individual level, it might be with regards to changes in anthropogenic access and activity levels during the harvest season similar to what has been observed in other predators (e.g., brown bears, *Ursus arctos*; Ordiz et al. 2012), with an expected shift in resource selection towards areas that are less accessible to humans and/or hounds. While we demonstrated this pattern in general, we were unable to resolve individual differences in selection for ruggedness as a function of anthropogenic access at the home range level. This might suggest cougar dependency on prey that migrates to lower elevations during the harvest season is more influential on space use than anthropogenic risk or that hounds are very effective regardless of terrain.

Alternatively, there are several factors that may have precluded our ability to identify an effect of anthropogenic risk on cougar space use. First, we may have selected poor metrics representing anthropogenic access and risk. Second, age and experience may represent a potential confounder given that all of our GPS-collared cougars were independent adults, with three individuals older than 10 years of age (Kaczensky et al. 2006, Ordiz et al. 2012). Thus, our sample of individuals may have already established a pattern of space use that changed little from year to year. Third, Monroe Mountains are heavily roaded by southern Utah standards, and are subject to relatively strong hunting pressure during the quota season and extensive recreational use during the non-hunting

season (*e.g.*, off-road vehicle use). Therefore, cougars within this system may exhibited limited behavioral plasticity having already undergone strong selection for avoidance behavior. And finally, over the course of the study, southern Utah experienced a sequence of mild winters which may have reduced hunter effort relative to more normal years, as cooler conditions prevent dogs from overheating and often retain more snow cover providing improved tracking substrate. Future assessments of cougar individual functional responses to anthropogenic activity will need to carefully consider the metrics used to capture human landscape use and the hypothetical response by individuals. Ideally, one will have the ability to incorporate harvested and non-harvested cougar populations, or experimentally control hunting pressure (*e.g.,* Stoner et al. 2006) which should provide improved resolution on potential anthropogenic effects on cougar space use.

In conclusion, documenting the movements of a predator in relation to its prey will be key to developing a more mechanistic understanding of space use for all interacting species. Contributing to these patterns will be increasing anthropogenic pressures that will shape the way these species interact. In turn, we will need to develop our understanding of how these species alter their space use patterns in response to anthropogenic pressures in order to inform our expectations of resource selection and associated species-specific habitat requirements in a landscape of change. Such an understanding will be key to successful management moving forward, whether of game species or species of conservation concern.

AUTHORS' CONTRIBUTIONS

PJM and JKY conceived the study. PJM lead the writing and conducted the analysis. PJM and JKY collected predator, lagomorph, and small mammal data. JKY and DS revised the manuscript. DS collected deer data.

DATA ACCESSIBILITY

We will make animal location data available upon publication.

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TABLES AND FIGURES

TABLE 4.1. Coefficients from a step-selection model for cougar space use. The ':' indicates an interaction between two or more variables. Harvest is a binary variable representing within (1) or outside (0) the cougar harvest season. Active is also a binary variable representing within (1) or outside (0) the active period of a day. VRM is the vector ruggedness metric. Elk and Deer Probability is the estimated relative probability of use by Elk and Deer, respectively. *Reference category is north aspect and no aspect.

Covariate Name	Coefficient	Robust SE	P-value
E*	0.091	0.029	0.002
S*	0.129	0.064	0.043
W*	-0.149	0.063	0.018
Slope	0.183	0.026	0.000
Slope^2	-0.104	0.014	0.000
VRM	0.053	0.015	0.000
VRM^2	-0.024	0.010	0.020
VRM:Harvest	0.084	0.033	0.010
VRM:Active	-0.024	0.014	0.083
(VRM^2):Active	-0.022	0.009	0.017
VRM:Harvest:Active	-0.069	0.025	0.005
Dist to Tree Cover	-0.538	0.094	0.000
Dist to Tree Cover^2	0.014	0.002	0.000
Dist to Roads	0.215	0.052	0.000
Dist to Roads^2	-0.083	0.025	0.001
Elk Probability	-0.045	0.062	0.472
Deer Probability	0.235	0.044	0.000
Dist to Tree Cover:Harvest	0.229	0.093	0.014
Elk Probability:Harvest	0.139	0.075	0.064
Deer Probability:Harvest	-0.243	0.051	0.000

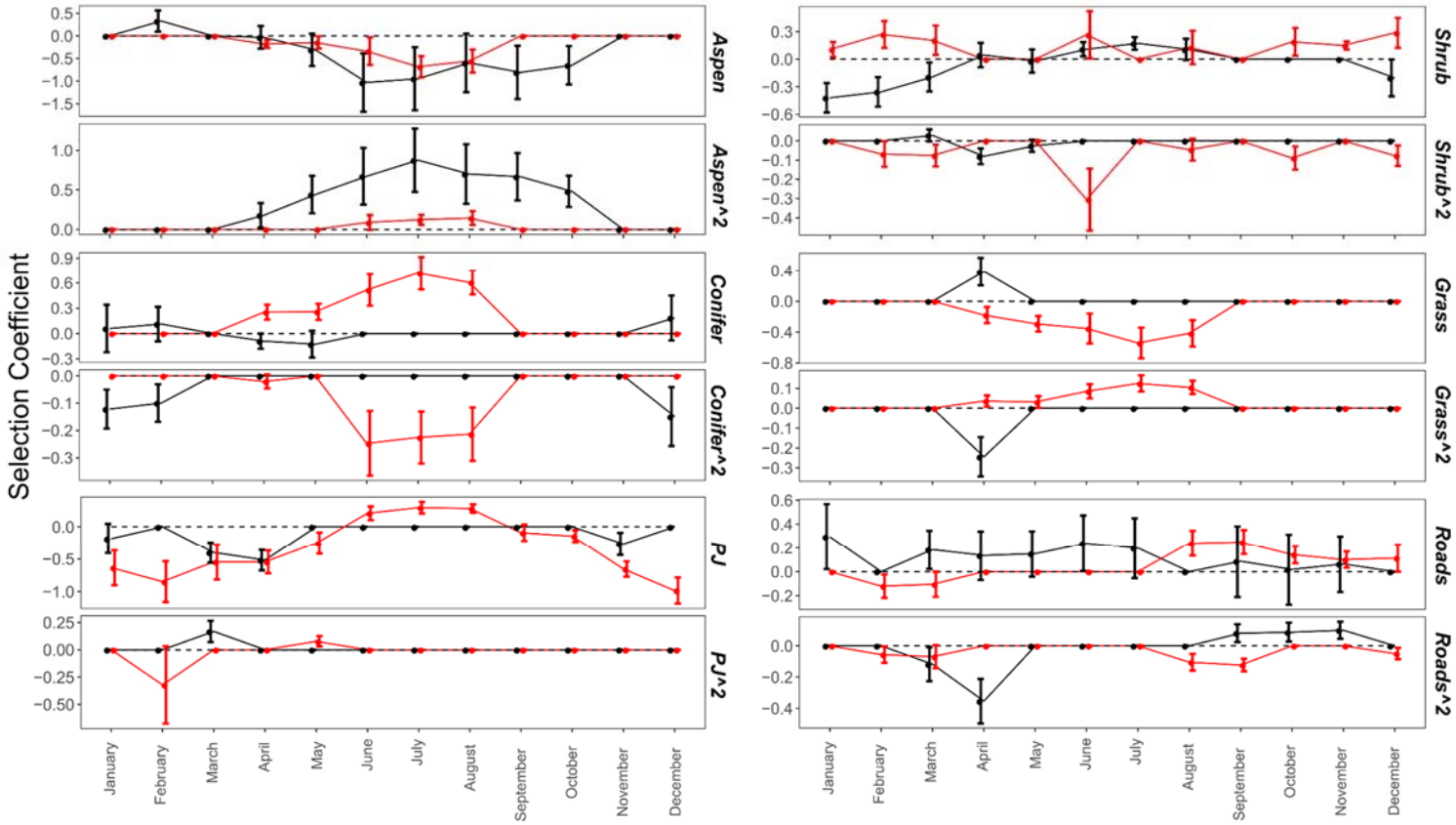

FIG. 4.1. The step-selection coefficients for key cover classes (and their 2nd order terms) in deer (black) and elk (red) estimated at monthly time steps. All metrics are measured as 'distance to'. Therefore, negative values represent selection and positive values avoidance. Error bars are the 95% confidence intervals. The trends do not include behavioral responses attributed to activity or time of day.

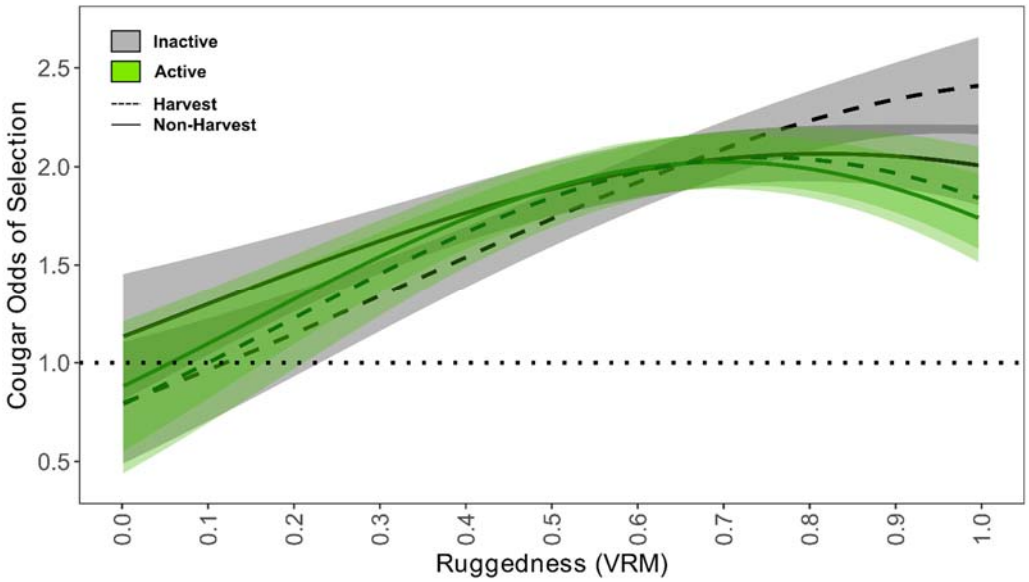

FIG. 4.2. Estimated odds of selection across the observed range of ruggedness (VRM) within cougar harvest (dashed) and non-harvest (solid) seasons, as well as during periods of inactivity (gray) and activity (green), in a study system in Fishlake National Forest, UT. Ribbons depict 95% confidence intervals.

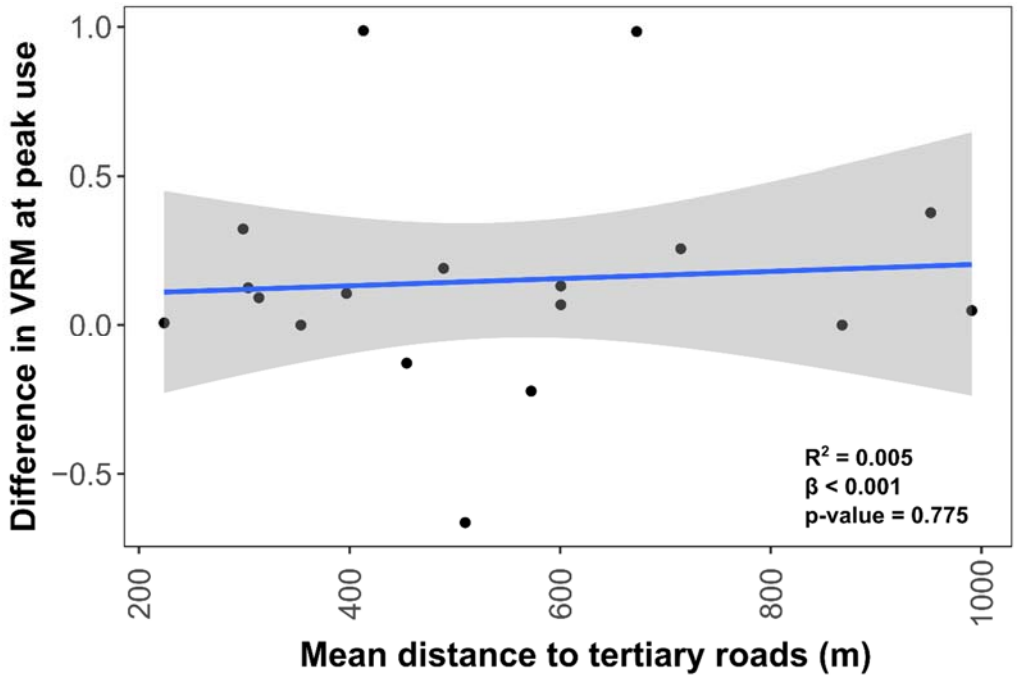

FIG. 4.3. The difference in VRM at peak probability of use (Inactive – Active) for each individual year as a function of mean distance to tertiary roads. Ribbon represents the 95% confidence intervals.

CHAPTER 5

UNCOVERING BEHAVIOURAL STATES FROM ANIMAL ACTIVITY AND SITE FIDELITY PATTERNS[4]

Summary

1: Space use by animals has important implications for individual fitness. However, resource requirements often vary throughout the course of a lifetime and are a reflection of the demands associated with daily tasks or specific life history phases, from food acquisition to reproduction, and emphasize the need to classify resource selection relative to specific behavioural states. Site fidelity is often indicative of behaviours important for individual maintenance (*e.g.*, foraging), species' life history (*e.g.*, seasonal site selection), social communication (*e.g.*, scent-marking), and species interactions (*e.g.*, predation, competition). Thus, resolving site-fidelity patterns associated with key behaviours is essential to accurately quantify behavioural-dependent resource needs and the fitness consequences of space use.

2: We propose a novel method for identifying site-fidelity patterns in animal location data using a convex hull clustering program called rASF. We also provide a means of integrating activity as a measure of behavioural state. We demonstrate the utility of the approach in identifying cougar (*Puma concolor*) predation events, coyote (*Canis latrans*) den and rendezvous sites, and coyote territorial boundaries.

3: We parameterized rASF based on site-fidelity characteristics that best characterized

[4] Mahoney, P.J. and J.K. Young. 2016. Uncovering behavioral states from animal activity and site fidelity patterns. *Methods in Ecology and Evolution*.

the clustering behaviour of interest and estimated behavioural state from either dual-axial accelerometer data or movement trajectory statistics. When behaviour was used in conjunction with cluster-specific metrics (duration, proportion of diurnal fixes, and landscape composition), we could accurately predict prey species associated with cougar kills and differentiate pup-rearing from scent-marking sites in coyotes.

4: Site-fidelity patterns and activities associated with animal revisitation will be key to identifying the behavioural motivations behind observed patterns of space use. Our approach provides an efficient, rigorous, and repeatable means of identifying site fidelity patterns associated with specific behavioural states without the need for direct observations, which are often impossible to collect at large spatial scales and in dense habitat. As such, this framework has significant potential to inform theory in behavioural ecology while providing managers with better resolution on appropriate management targets associated with key aspects of a species' life history.

Introduction

Understanding the behavioural motivations underlying observed patterns in animal movement is a central theme in behavioural ecology (Nathan 2008). Importantly, animal movement and space use are relevant to an individual's fitness and manifest as the aggregation of behavioural trade-offs made by the organism throughout the course of a lifetime. However, the resource requirements for self-maintenance (*e.g.,* foraging, refuge, etc.) and reproduction are often disparate, emphasizing the need to distinguish relevant behaviours when classifying resource selection (Owen-Smith *et al.* 2010; Roever *et al.* 2014; Bouyer *et al.* 2015). Failing to do so can lead to biased expectations of resource use

or confound our understanding with regards to the specific resource needs of a species (Roever *et al.* 2014). Further, accounting for behaviour in assessments of resource use are vital to improve our comprehension of selective pressures shaping populations through the demographic consequences of animal space use in changing environments (Tuomainen & Candolin 2011; Johnson *et al.* 2015; Childs *et al.* 2016).

However, resolving the link between animal space use and behaviour is limited by our ability to observe individuals in wild settings without measurable observer effects. Advancements in tracking technology have led to decreases in relocation intervals such that animal activity can be inferred from an animal's movement trajectory (Gurarie *et al.* 2009, 2016; Beyer *et al.* 2013). In addition, many tracking platforms are being outfitted with sensors (*e.g.,* accelerometers or gyrometers; Wilmers *et al.* 2015) capable of collecting data on fine-scale directional movement in two or three dimensions and can also be used as a measure of animal activity. Measures of activity are often used to classify behaviour into states, or behavioural patterns of extended duration (Martin & Bateson 2007). Thus, activity data, derived from technology or direct observations, are necessary for empirical evaluations of behaviour and can be used in conjunction with animal relocation data (*i.e.*, spatial data) to classify an animal's behavioural state and associated resource utilization (Nams 2014; Abrahms *et al.* 2015).

Ideally, researchers should correlate observed behaviours with recorded patterns in activity through supervised statistical procedures (*e.g.*, Nathan *et al.* 2012; Wang *et al.* 2015). However, observing wild-type behaviours is difficult to impossible in most systems. Thus, evolving technologies and analytical methodologies will play a key role in permitting researchers to pursue lines of inference related to behavioural motivation and

the fitness consequences of animal space use (Wilmers *et al.* 2015). One such alternative is to capitalize on unsupervised statistical techniques for inferring behaviour from sensor-derived activity data. Current unsupervised methods can provide a coarse metric for behavioural state through classification of animal path metrics. Such methods include multi-state random walk (Morales *et al.* 2004; Beyer *et al.* 2013) and behavioural change point analysis (Gurarie *et al.* 2009, 2016). While animal trajectories can provide useful insight into an individual's behaviour at a given location, path metrics may be too coarse in contexts where the interval between relocations is prohibitively long, precluding our ability to resolve transitions between behavioural states. In such cases, directional sensor data can help to fill the gaps by providing finer temporal resolution on activity with minimal impacts to hardware battery life (Gao *et al.* 2013). However, only a few unsupervised methods can be extended to evaluate directional sensor data alone or in conjunction with animal relocation data (Nams 2014; Gurarie *et al.* 2016).

In cases where coarse estimates of behavioural state (*i.e.*, resting, moving, and foraging) are sufficient, unsupervised statistical methods can be a useful tool for classifying behaviours associated with relevant space use patterns. For example, many species exhibit some level of site fidelity (*i.e.*, clustering), which is often indicative of behaviours important for individual maintenance (*e.g.*, foraging; Wakefield *et al.* 2015), a species' life history (*e.g.*, migration and seasonal site selection; Teesdale *et al.* 2015), and social communication (*e.g.*, scent-marking; Allen *et al.* 2015), as well as community and ecosystem-level processes (*e.g.*, predation; Smith *et al.* 2015; Ebinger *et al.* 2016). While identifying behaviours associated with high-fidelity sites may be straightforward in some species (Wakefield *et al.* 2015), for others it is difficult to tease apart which sites are

correlated with specific behavioural states using raw relocation data alone. Provided there is sufficient spatial and temporal resolution, behavioural states associated with a given high-fidelity site can be estimated using activity data and one of several unsupervised methods. We can then better inform our assumption of behavioural states associated with site-specific fidelity patterns, while potentially improving our inference and predictions of species-specific behaviour (*e.g.*, predation and reproduction) within the context of site fidelity through time.

We propose a novel method for identifying site-fidelity patterns from animal relocation data using a program call rASF (R Animal Site Fidelity). rASF implements a clustering algorithm based on local convex hulls and provides functionality to integrate estimates of activity as derived from trajectory statistics or directional sensor data. Here, we demonstrate the utility of the approach in identifying a range of site-fidelity patterns while linking estimated behavioural state derived through unsupervised behavioural change point procedures (Gurarie *et al.* 2009) and k-means clustering of activity data. We implement three case-studies representing a range of plausible site-fidelity patterns by resolving the location of 1) predation events (short-term, high intensity of use), 2) reproductive sites (variable duration, moderate to high intensity of use), and 3) territorial boundaries through conspecific marking sites (long-term, low intensity of use) using a combination of clustering procedures and expected behavioural states associated with the identified locations. In case 1, we use relocation and directional sensor data to identify predation events in mountain lions *Puma concolor.* In case 2, we identify den and rendezvous sites in a strongly territorial species, coyotes *Canis latrans*, using a combination of relocation and directional sensor data. In case 3, we demonstrate how site

fidelity can inform our expectations of home range by identifying presumed territorial marking sites of coyotes (Wilson & Shivik 2011), and use associated trajectory-based activity to inform behavioural state of the individuals while at marking sites. rASF can be used to partition data by site-fidelity pattern, behavioural state, or a combination of fidelity and behavioural state to permit assessments of the associations between landscape composition and site fidelity, as well as variation within and between individuals.

Materials and methods

CLUSTER IDENTIFICATION

The program rASF is coded in R (v.3.2.4; R Core Team 2016) and uses local convex hulls to resolve behavioural clustering events (see Data Accessibility below). Users specify four parameters that reflect the desired scale of site fidelity: 1) the minimum number of locations ($N_{total} = 1_{focal} + N_{revisits}$), 2) the maximum spatial distance between two locations, 3) the time interval length between locations, and 4) whether to constrain time as within or outside a given interval in order for a point to be included within a cluster. The software loops through every location within a time series, clusters locations that meet the user-defined criteria, draws a convex hull around each individual cluster of points, and merges (*i.e.*, unionizes) all hull clusters that overlap in space and time (Fig. 1). These procedures generate cluster-specific utilization distributions located throughout an animal's home range. The output includes cluster-specific data, such as cluster duration, cluster area, number of points, and spatial output for use in GIS software, statistical analysis, or both. As the number and size of clusters can be sensitive

to the parameter inputs, we recommend an evaluation of cluster sensitivity to pre-defined parameters, as well as visual inspection of the output, for a range of parameter values. Although not necessary for use with this methodology, rASF incorporates methods that permit integration with activity data, allowing the user to define cluster-specific behaviour qualitatively or empirically.

INCORPORATING ACTIVITY

Raw activity data can be stored in one of several ways: 1) as a single affiliated time series (sensor- or trajectory-based), 2) as a window of time around a given cluster or point (sensor), or 3) aggregated activity by points within cluster (sensor- or trajectory-based). The R code we have developed for the rASF (see Data Accessibility below) provides an efficient means of integrating cluster output with the behavioural change point analysis approach described in Gurarie et al. (2016) and implemented in the R package *bcpa* (v.1.1; Gurarie 2014). In brief, the behavioural change point analysis (hereafter BCPA) uses a moving window with a user-defined window size to classify a single 'likely' change point – or transition in behavioural state – within each window along an activity time series. Change points are classified using one of eight likelihood models ranked by Bayesian information criterion (BIC) representing all combinations of mean activity (μ), standard deviation in activity (σ), and characteristic time-scale of autocorrelation (τ) in activity. The characteristic time scale captures the temporal range of autocorrelation in activity and is dependent on the time interval between measurements (*i.e.*, the unit of time, Gurarie 2014). The window size is effectively a tuning parameter whereby smaller windows permit the estimation of finer scale transitions in behavioural

state. However, Gurarie (2014) recommends a minimum window size of 30 steps, which appears to be the lower limit for model convergence under most scenarios.

BCPA takes a single activity variable stored as a time series and is often a composite metric derived from movement-based statistics. A commonly used, movement-based composite metric is persistence velocity as defined by equation 1., where *V* is velocity, or the estimated movement rate, between time *t-1* and t. θ is the turning angle centred on 0 (vector trajectory from *t-2* to *t-1)* at time *t*.

$$\text{Eqn 1. } V_p = V * cos(\theta)$$

We provide a slight extension in rASF to permit greater ease of incorporating activity metrics derived from directional sensor data into BCPA. One recommended composite metric for directional sensor data is the Vector of Dynamic Body Acceleration (VeDBA) defined in equation 2 (see Qasem *et al.* 2012 for additional details). Variable A is acceleration along the *x*, *y*, and *z* axes as measured by directional sensors.

$$\text{Eqn 2. } VeDBA = \sqrt{({A_x}^2 + {A_y}^2 + {A_z}^2)}$$

Smoothing sensor data along each axis by a running average is often recommend to help account for gravitational bias before analysing directional sensor data (Qasem *et al.* 2012). However, we do not use the raw or composite metrics directly, but instead rely on BCPA outputs which can include a smoother derived from a moving window.

Importantly, directional sensor data can be difficult to manage as quality, quantity, and post-processing can vary significantly between hardware manufacturers. It is best to choose the platform (or manufacturer) with the greatest amount of user control over directional sensors if activity data is a priority. However, activity was not of primary

concern in the studies presented here; therefore, we utilized the dual-axis accelerometer sensors in our existing GPS collar platforms (*i.e.,* $A_z = 0$ in Eqn 2).

CASE-SPECIFIC METHODS AND RESULTS

Case 1: predation - short-term, high intensity fidelity

We demonstrate how the clustering program can be used to identify predation events with relocation and activity data (directional sensor) derived from movements made by two adult female cougars during 2014 and 2015. The data were from a four-year study (2012 - 2015) on Monroe Mountain, Fishlake National Forest in southcentral Utah. All cougars were treed using hounds, immobilized with Ketamine and Xylazine (with weight-dependent doses), and fitted with Lotek GPS collars (Model GPS3300S; Lotek, Newmarket, Ontario, CA) containing dual-axis accelerometers following pre-approved animal care protocols (Utah State University IACUC protocol #2182). We programmed all cougar collars to log five minute averages for X and Y-directional activity with a 4-hour GPS relocation interval. The collars were a store-on-board design, necessitating cougar recapture after a year or more of deployment in order to recover all data. Thus, we often attempted to locate kills made by our study animals 2-18 months after the predation event occurred. The clustering program allowed for rapid batch processing of collar data as soon as collars were in hand, permitting quick turnaround and a list of candidate kill clusters for technicians to investigate. We used a minimum fix count of three relocations, a spatial buffer of 100 meters, a temporal buffer of 72 hours, and included all locations that were within the 72-hour time interval. Our biological justifications for these parameter values were the desire to resolve any cluster with a minimal residency of eight

hours (≥3 fixes), to identify clusters of points that could accommodate resting sites near predation events (≤100 meters based on observations from the field), and to allow residency flexibility over a rolling window of 72 hours based on observed ungulate prey handling times. The number of clusters identified were relatively insensitive to perturbations in these values. Due to time constraints, crews were only able to visit a random subset of clusters for each individual during the summer of 2015 (Table 5.1). The species, sex, and age of prey were identified where possible.

Next, we integrated activity data as derived from accelerometers by calculating VeDBA and estimating BCPA for the activity time series. We used the change point statistics to classify behavioural state(s) associated with each cluster using k-means clustering (Zhang *et al.* 2015). The number of k-means clusters was estimated using the R package *NbClust* (v.3.0; Charrad *et al.* 2014), which uses 30 different metrics to assess the appropriate number of clusters for the data. We then used our subset of visited clusters to predict the occurrence of mule deer, elk, or other (beaver, *Castor Canadensis*; coyote; domestic sheep, *Ovis aries*; and domestic cattle, *Bos taurus*) prey species using classification-based random forest (R package *party*, v.1.0-25; Strobl *et al.* 2008) with cluster-specific characteristics and BCPA-derived activity as predictors. Cluster-specific characteristics included duration, proportion of nocturnal fixes, and cougar ID, as well as landscape features such as elevation (USGS 30-meter DEM, 2010), terrain ruggedness index (Riley *et al.* 1999), distance to shrub cover (≥ 30%, LANDFIRE 2012), distance to tree cover (≥ 50%, LANDFIRE 2012), and aspect (cardinal direction).

We visited 87 potential kill clusters and identified a total of 69 prey remains (Table 5.1). BCPA visualizations of predation clusters were qualitatively distinct between

the two primary ungulate prey, mule deer *Odocoileus hemionus* (Fig. 5.2, fawn and adult in Clusters 10 & 16, respectively), and elk *Cervus elaphus* (Fig. 5.2, Cluster 18). The timing of points within clusters, the duration of clusters, and the activity immediately following cluster initiation appear to be good indications of whether or not a kill occurred at a given site (Fig. 5.2; Table D1). We were able to identify four behavioural states using the dual-axis accelerometer data, BCPA output (τ_{unit} = 5 minutes), and k-means clustering (Table 5.2). The first behavioural state is indicative of low activity or resting. States two and three are distinguishable from one another by the characteristic time-scale of autocorrelation, represented by the coefficient τ, and reflect differences in the consistency of movement at moderate levels of activity. Thus, state two may reflect more dynamic movement attributable to reduced duration of autocorrelation at moderate levels of activity (State two: 47.9 minutes; State three: 142.3 minutes). However, states two and three are likely reflective of behaviour associated with sustained levels of moderate activity where more directed or rhythmic movements are a component, such as walking and possibly feeding after a kill is made (see below). State four represents higher levels of activity, likely associated with higher rates of travel or hunting.

We could not use random forest to predict the occurrence of predation events using output from rASF as one or more kills were identified at 69 of 87 clusters visited (79.3 %), constraining our sample of undetected or non-predation sites. Thus, we limited our assessment to predicting prey species at identified kill sites using site- and cluster-specific characteristics. Even with a relatively small sample of kill sites and low-resolution directional sensor data (*i.e.,* dual-axial vs. tri-axial accelerometer data), random forest maintained 71% accuracy (1 – 'out-of-bag' error) in predicting prey

species using 17 predictor variables (Fig. D1). Importantly, the most influential predictor variables included cluster duration and proportion of nocturnal fixes, as well as the SD in VeDBA, median and SD in the time-scale of autocorrelation after cluster initiation (eight hours post-initiation), and SD in the time-scale of autocorrelation before cluster initiation (four hours pre-initiation, Fig. D1). Random forest performed well in predicting deer kills (90%; n = 42), moderately well for elk (50%; n = 22), and very poorly for all other species (0%; n = 5; Table D2).

Case 2: reproduction - intermediate fidelity

We further demonstrate the ability to tune rASF to identify sites of moderate-to-high intensity of use over longer periods of time than typically associated with predation events. As an example, we use the clustering software to identify the occurrence, timing, and location of denning and rendezvous sites in coyotes. This dataset was also derived from the four-year study (2012 - 2015) on Monroe Mountain, Fishlake National Forest in southcentral Utah. Coyotes were captured using either contracted helicopter net-gunning during the winter or padded leg-hold traps (Victor #3 soft catch) fitted with tranquilizer tab devices (TTDs containing Propriopromazine, Balser 1965) during the remainder of the year. Coyotes were fitted with Lotek GPS collars (Model GPS6000) containing dual-axis accelerometers, which were programmed to log five-minute averages for X and Y-directional activity and 6-hour GPS fix intervals from the end of August through May and 3-hour GPS fix intervals from the June through the end of August. The capture and handling protocols were approved by IACUC (Utah State University IACUC protocol #2182). All individuals were released at the site of capture.

We illustrate the approach with a single reproductive male using a subset of data from March through August of 2014, the time period for pup rearing prior to the initiation of pup dispersal in the Fall (Harrison *et al.* 1991; Gese *et al.* 1996). We used a minimum number of five fixes, a spatial buffer of 50 meters, a temporal buffer of 10 days, and selected locations that occurred within the specified time interval. Here again, we chose parameter values to help resolve frequent revisitation over the duration of their site-specific use (≥5 fixes), to incorporate clusters of points that could accommodate pup movement or adult bedding sites (<50 meters), and to allow flexible but extended residency over a rolling window of 10 days. As with the cougar clusters, the number of clusters identified were relatively insensitive to perturbations in these values, with the possible exception of the minimum number of fixes. However, we chose an intermediate value of five here to capture short duration rendezvous sites near the end of the summer at the risk of identifying too many sites that were not reflective of pup caching sites. We integrated activity as described for the predation clusters above.

The output from rASF identified 12 potential pup-rearing sites. The k-means clustering diagnostics supported three behavioural states, indicative of low, moderate, and high activity levels (Table 5.2). The natal den (*i.e.*, Cluster 1; Fig. 5.3) was confirmed through ground-truthing via radio telemetry in late May of 2014. The male remained in the area of the natal den for at least 19 days before the pups were moved approximately 830 meters to the northeast. However, we were only able to confirm a single maternal den (Cluster 2; Fig. 5.3) and rendezvous site (Cluster 5; Fig. 5.3). Moderately long residency (≥1 week) with a high prevalence of diurnal points and low-to-moderate activity were indicative of den and rendezvous sites (Table D3; Andelt *et al.* 1979).

Case 3: territoriality - long-term, low intensity fidelity

To demonstrate a third utility of the software, we used rASF to identify possible territorial marking sites visited by coyotes for communicating with neighbouring conspecifics. The third dataset consisted of coyote relocation data from south-eastern Idaho on the Idaho National Engineering Laboratory during 2005. All individuals were captured using helicopter net-gunning and fitted with Lotek GPS collars (Model 3300S) following the handling protocols outlined in the National Wildlife Research Center QA-1025. Although these collars did not contain directional sensors, they were programmed with 5-minute location intervals permitting the estimation of fine-scale, trajectory-based activity data. In this case, we expected infrequent but periodic revisiting of sites by coyotes. Thus, we switched from clustering locations within a time interval, as we did for the other two cases, to identifying spatially associated locations that occurred over a longer period of time and that represented revisitation after a predetermined time interval had transpired. We used a minimum number of three fixes, a spatial buffer of 25 or 35 meters, and clustered only those locations that occurred after five days. We selected parameter values to help identify any site with a minimum of three fixes given the short duration of collar deployment (<2.5 months), a small spatial buffer to resolve fine scale (point) space use while accommodating GPS error, and a temporal interval to permit capture of coyote movement patterns within a home range indicative of territorial patrol (≥ 5 days based on field observations). The number of clusters identified were relatively insensitive to perturbations in all except for the minimum number of fixes. Further, we anticipated these sites to be associated with intermediate-to-high levels of activity (*i.e.*,

non-resting sites) with moderately directed movements (*i.e.*, territorial patrolling). Thus, we integrated activity as we did above, but now by using trajectory-based statistics with persistence velocity as our composite metric in the BCPA. After estimating cluster sites by pack (N_{Packs} = 6, N_{HRs} = 12 across two time periods), we generated concave hulls around the outermost cluster centroids as a representation of territorial boundaries (hereafter denoted territories). We estimated percent area overlap and median gap distances along shared borders for each concave hull territory using ArcGIS (v.10.2.2; ESRI 2016).

For comparison with more typical home range estimators, we generated pack-specific home range estimates using kernel density in the R package *adehabitatHR* (v.0.4.14; Calenge 2006) with an ad-hoc bandwidth estimator and a bivariate normal kernel. We calculated kernel home range overlap based on percent area shared between each neighbouring territory as two dimensional home ranges are often used to estimate availability in resource selection functions. Finally, for each cluster-generated territory, we intersected the concave hull estimates with the pack kernel density rasters using R package *raster* (v.2.5-2; Hijmans 2012) to identify percent volume encompassed by the concave hulls (*i.e.,* isopleth).

We estimated 10 coyote pack home ranges over two consecutive periods from winter through summer of 2005. Animal locations and home ranges (95-99% KDE) overlapped in all cases where neighbouring packs were monitored. Constraining home range boundaries to the outermost high-fidelity sites as identified by the clustering software reduced perceived home range overlap considerably, from 13.9% (SD = 7; 99% isopleth KDE) to 0.3% (SD = 0.4; Concave Hull; Tables D4 & D5), while maintaining a

median gap distance between territories of 244.5 meters (SD = 118.7; Table D6). Further, 66.9% (SD = 0.21) of the high-fidelity clusters along a shared boundary were visited (≤ 35 meters) by neighbouring conspecifics within the two- to three-month period collars were deployed. The territories identified by high-fidelity clusters represented 89.8% (SD = 0.06; Table D7) of the total kernel utilization distribution volume and captures approximately a 90% KDE isopleth, though the home range shapes likely vary in important ways (Fig. D2). Although collared non-resident individuals were rare, one individual was a non-resident for most of the monitoring period and exhibited movements that were largely constrained by the high-fidelity clusters identified (Fig. 5.5).

Discussion

We demonstrated the utility of our program in identifying sites with high fidelity as determined by user inputs under a number of scenarios. In our first case, we identified predation events by clustering cougar locations in space and time. While spatiotemporal clustering in animal relocation data is commonly used to identify predation events (Anderson & Lindzey 2003; Elbroch & Wittmer 2013; Ebinger *et al.* 2016), few methods are explicitly programmed, incorporate clustering in space and time, or provide an efficient and objective means of incorporating activity data. Thus, our method provides a more comprehensive view of a potential predation event by achieving all three components, while providing quick and repeatable output from large quantities of relocation data. However, we caution against visiting potential predation sites based solely on, or even in conjunction with, estimates of behaviour as derived from unsupervised activity. Our recommendation is to visit all or a random subset of clusters to

ensure all relevant foraging events are observed during the monitoring period. In cases where researchers rely extensively on activity data during the kill cluster investigation phase, scavenging events might go unobserved while favouring larger prey and in turn significantly underrepresenting the caloric intake of the individual (Elbroch *et al.* 2014). Provided sufficient quality, resolution, and sample size, data gathered during cluster visits, along with cluster-specific metrics (*e.g.,* duration, number of nocturnal fixes, etc.), site characteristics, and associated activity metrics, can be used to develop predictive models for estimating the probability of kill occurrence and prey type at all remaining unvisited cluster sites.

In our case, we did not have sufficient data to estimate the probability of cougar kill occurrence based on cluster and site metrics. However, rASF performed well at resolving predation events, even of smaller prey species such as beaver and coyote, with 79% of visited clusters containing identifiable kills. We recognize that detection of carcasses contributed to this number and was likely influenced by prey type, cover class, and the time that transpired since a kill occurred (mean = 52.4 weeks, SD = 15.4). Although we did not rigorously assess detection, incidental cluster revisitation by two crews indicated kill detection rate is likely around 80% (n = 5). We had some success predicting individual prey species, particularly mule deer, based on cluster metrics and animal activity using random forest. However, small sample sizes, multiple kills in some clusters (*e.g.,* mule deer doe and fawn or elk cow and calf), and variability in size associated with the 'other' category likely reduced the predictive power in the current assessment. Further, young elk (calves and yearlings) were disproportionately represented in the diet (66.6%) and may overlap with adult deer in terms of biomass,

potentially limiting our predictive accuracy in our smaller sample of elk. We attempted to include age class in our random forest response variable, but this resulted in higher out-of-bag error rates and reduced predictive accuracy.

This then begs the question should we expect to see differences in activity associated with a variety of prey types. While the answer is likely system-specific, in our case measures of activity, or VeDBA, also proved informative for distinguishing prey species even after accounting for duration of time spent at a kill (Fig. D1). For context, a kill is often followed by reduced levels of activity and extended periods of autocorrelated movement distinguishable from resting sites, and is supported by qualitative assessments of cluster-specific BCPA time series (Fig. 5.2). Thus, support for variation in activity and the time-scale of autocorrelation before (4-hours) and after (8-hours) cluster initiation may suggest differences in activity associated with the capture and handling of the two ungulate prey species (Fig. D1). Therefore, we expect that larger sample sizes, added directional sensor resolution (*e.g.,* tri- versus dual-axial accelerometers, finer temporal measurements), and finer spatial fix rates for better resolution on the timing of a kill will likely improve the predictive accuracy in a predation event context.

In the second scenario, we investigated more intermediate duration and use of locations with high fidelity by identifying den and rendezvous sites (*i.e.*, pup-rearing) from a single male coyote. While using data derived from a breeding female may have been more informative, particularly after she emerges from the natal den and permits GPS satellite acquisition and data transmission, we chose relocation data from a breeding male to demonstrate the efficacy of the method in circumstances where the data may be less clear. In this case, activity and estimates of behavioural state provided additional

evidence for the existence of pup rearing sites. The male's behavioural data indicated low to moderate activity with largely daytime visitation at all early- to mid-season sites. This matches our expectations based on knowledge of coyote behaviour where we might anticipate crepuscular or nocturnal foraging by breeding males and other non-breeding pack members with food provisioning for denning females and reduced activity during the daytime while present at pup-rearing sites (Bekoff & Wells 1982). In addition, rASF identified a total of 12 clusters, a number of which were in close proximity to one another and may reflect greater mobility of pups during mid-to-late summer. Thus, based on timing and spatial occurrence, these 12 sites could likely be reduced to six total sites, two den and four rendezvous sites (Table D2). Although the above is intuitive, once the location and timing of these sites have been identified, from here one could investigate other life history and behavioural metrics such as reproductive phenology, food provisioning rates by males, number of pup rearing sites, and duration of residence at each site as influenced by resource availability, climate change, and measures of human disturbance.

In the last case, we demonstrate the utility in identifying sites of long-term, low intensity use with periodic revisitation by individuals. More specifically, we derived realized territories based on biological patterns associated with potential conspecific signalling and knowledge of scent-marking behaviour in coyotes (*i.e.,* scent marking such as urine, faeces deposition, and scratching). And while scent-marking along the margins of a territory do not prevent intrusion, they serve to orient individuals in space and most frequently occur at the margins of a territory and in areas with the highest intrusion rates (Wells & Bekoff 1981; Gese & Ruff 1997). Although we did not ground-truth the sites

identified by the clustering software as true scent-marking sites in the Idaho population, we believe multiple lines of evidence indicate that these locations effectively demarcate territorial boundaries, including periodic revisitation by individuals within a pack (≤ 35 meters), visitation by neighbouring conspecifics (Gese & Ruff 1997), very little overlap of high-fidelity sites between neighbours along narrow boundary margins (Kamler & Gipson 2000; Wilson & Shivik 2011), moderate- to high- activity levels at nearly all outermost clusters (indicating animals on the move), and a single non-resident individual that exhibited movements largely constrained by these interstitial spaces between territories during the same time period (Kamler & Gipson 2000). While a more rigorous assessment is needed, these results suggest using site-fidelity patterns in territorial species could lead to more biologically-informed estimates of territory. Further, more explicit assessments of territoriality with respect to conspecific marking in the context of animal space use and movement could lead to an improved understanding of the mechanistic processes leading to home range emergence (Moorcroft *et al.* 2006). Finally, while we focused on establishing the link between patterns in site fidelity, social cues, and territorial margins as proof-of-concept, this approach can easily be extended to identify any locations where low intensity of use but periodic revisitation is expected (*e.g.,* watering sites, social marking sites, mineral acquisition sites, etc.).

Only recently has the importance of including behaviour or behavioural state in resource selection been demonstrated (Roever *et al.* 2014). While we do not explicitly address resource selection in the cases described above, one could easily implement our method to quantify the associated landscape features and phenology of behaviours that lead to high levels of fidelity at ecologically-important sites. Behaviourally-unaffiliated

resource selection functions are likely to wash out the importance of low-use sites with significant resource value (*i.e.,* social marking sites). Thus, differentiating these ecologically-important sites based on fidelity patterns will permit researchers to explicitly assess selection of low-use sites by means of site-specific characteristics (*e.g.,* scent-marking with respect to known movement corridors). Establishing this link will not only improve our predictions of resource selection, but will be essential to developing our understanding of individual variation in space use behaviour and the fitness consequences of resource selection.

In conclusion, we recognize the field of movement ecology is rapidly evolving, specifically with respect to behavioural classification from animal relocation data. And while we plan to further develop our software to meet the needs of end users and promote more general use of our clustering software by incorporating additional options for behavioural classification (*e.g.*, hidden Markov models, Jonsen *et al.* 2013), the current version provides an efficient, rigorous, and repeatable means of identifying site fidelity patterns associated with specific behavioural states. As such, the software has significant potential to inform theory in behavioural ecology while providing managers with better resolution on appropriate management targets associated with key aspects of a species' life history (*e.g.,* Abrahms *et al.* 2015).

Data Accessibility

The GPS and activity data used in this study are available on Movebank (movebank.org, study name : Site fidelity in cougars and coyotes, Utah/Idaho USA) and are published in the Movebank Data Repository with doi:10.5441/001/1.7d8301h2.

R code and a vignette with datasets: GitHub/Zenodo doi:10.5281/zenodo.61429. For most current version, visit https://github.com/PMahoney29/rAnimalSiteFidelity.

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Tables and Figures

Table 5.1. The total number of clusters identified, number of clusters visited, and number of prey by species (values in parentheses are percentages) for two adult female cougars (F53 and F64) on Monroe Mountain, Fishlake National Forest, Utah during 2014 and 2015.

	F53 (%)	**F64 (%)**
Total Clusters	89	109
Visited Clusters	35	52
Number of Clusters w/Prey	24 (69)	45 (87)
Total Prey Found	30	53
Number of Elk	7 (23)	16 (30)
Number of Mule Deer	21 (70)	34 (64)
Number of Other	2 (7)	3 (6)

Table 5.2. The estimated centroids of all three BCPA statistics, $\hat{\mu}$ (mean of VeDBA), $\hat{\sigma}$ (standard deviation of VeDBA), and $\hat{\tau}$ (time-scale of autocorrelation in VeDBA), for all k-means clusters representing four possible behavioural states in cougars and three possible behavioural states in coyotes. The unit for the characteristic time-scale is 5 minutes, as reflected by the interval of time between activity measurements.

	Cougar			**Coyote**		
Behavioural State	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\tau}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\tau}$
1	6.93	8.53	3.06	80.96	101.72	38.37
2	33.58	39.29	9.57	166.85	88.84	12.90
3	29.39	41.12	28.45	13.01	24.70	6.48
4	81.55	59.06	6.12	-	-	-

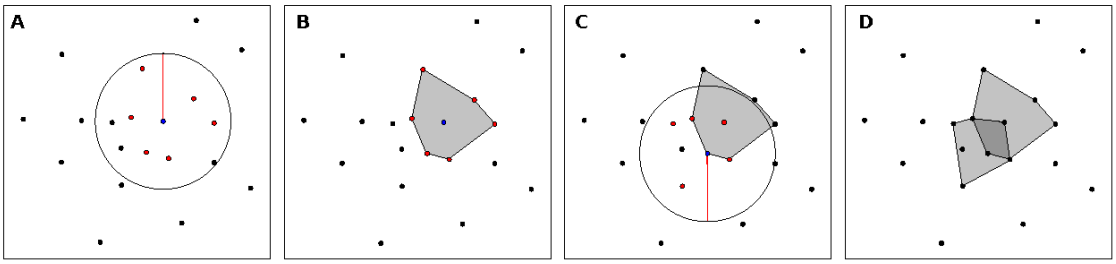

Fig. 5.1. A schematic of the cluster identification process in chronological order. The process first (A) identifies all points that occur within the spatial buffer (red line) and time interval (red points), (B) identifies the convex hull of 'clustered' points, (C) moves to the next point in the time series and repeats the process, and ultimately (D) stacks overlapping polygons (in time and space) into a single cluster.

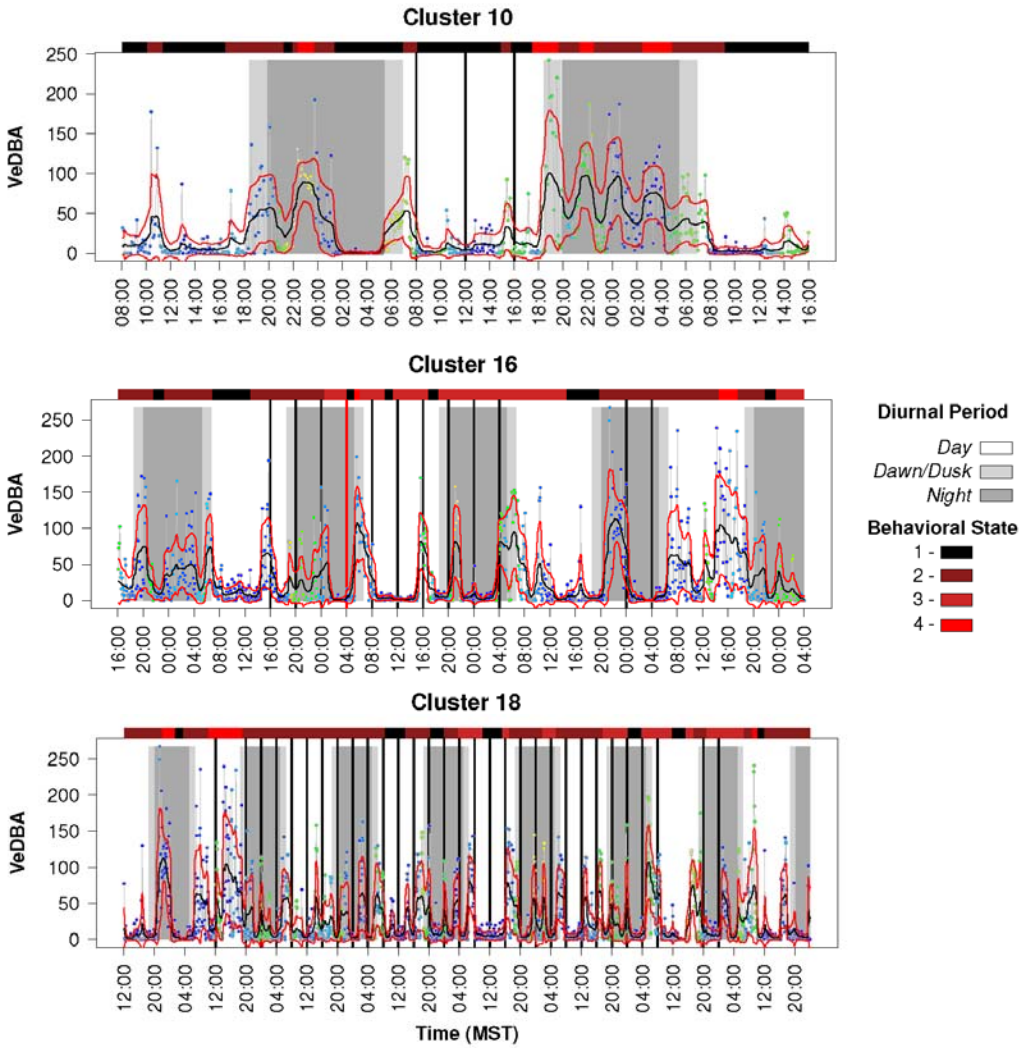

Fig. 5.2. Three representative clusters derived from GPS relocations of a single female cougar (F53) with a 24-hour buffer at the start and end of the cluster windows. Vertical black bars represent GPS fixes and vertical red bars represent missed GPS fixes. The colored points are a BCPA time series of VeDBA activity derived from a dual-axis accelerometer at 5-minute intervals, with colors from blue-to-yellow corresponding to low-to-high autocorrelation. The band at the top of each cluster identifies the behavioral state (more red equates to higher activity) estimated from k-means clustering using the BCPA metrics. Daylight patterns are depicted in grey-shaded bands in the plot background. Cluster 10 is typical of a mule deer fawn (note all daytime fixes), Cluster 16 of a mule deer predation event, and Cluster 18 of an elk predation event.

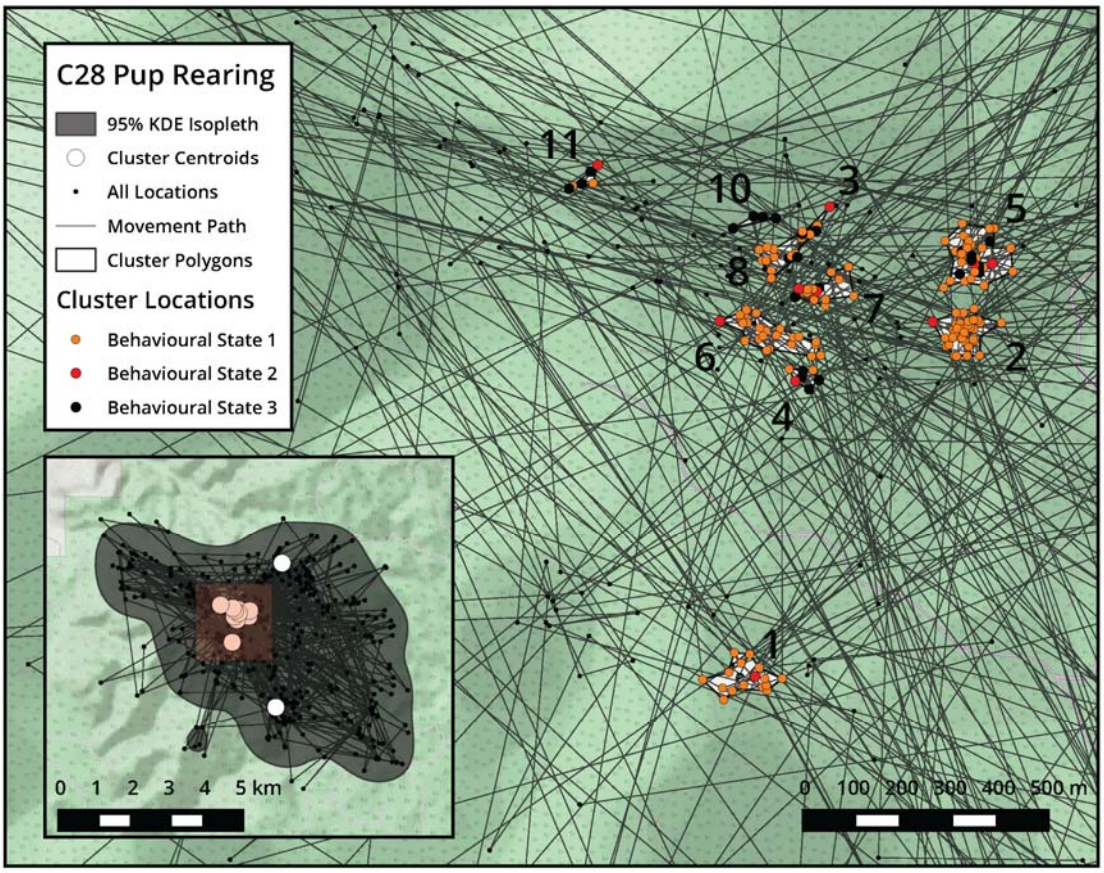

Fig. 5.3. The points associated with clusters identifying den and rendezvous sites in a high-elevation coyote pack within the Monroe Mountains, Utah. Inset shows the location of the clusters within the pup-rearing seasonal home range. Cluster 1 is the natal den site, cluster 2 is a maternal den site, and clusters 5 and 11 are rendezvous sites. The remaining clusters (3, 4, 6, 7, 8, and 10) represent a combination of possible rendezvous sites that likely depict significant pup movement.

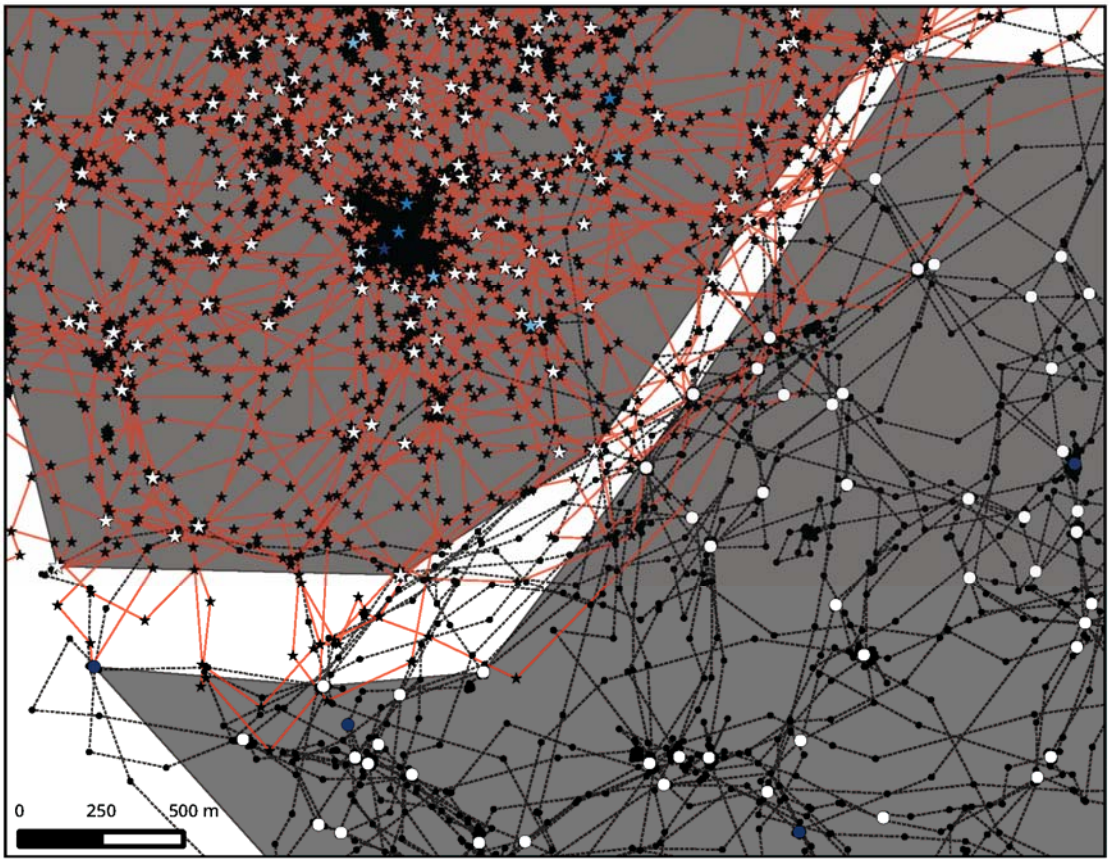

Fig. 5.4. A boundary between two neighboring coyote packs at the Idaho National Engineering Laboratory during the winter of 2005, as identified using rASF. The polygons are 100% concave hulls around all active cluster centroids in an effort to capture the boundary in its truest form. The smaller, black stars and circles depict the locations from two neighboring coyote individuals. The larger icons represent cluster centroids for each individual (stars and circles, respectively; blue ~ least active, white ~ most active). Paths for each individual are included to demonstrate how they move in response to the space use of their neighbor.

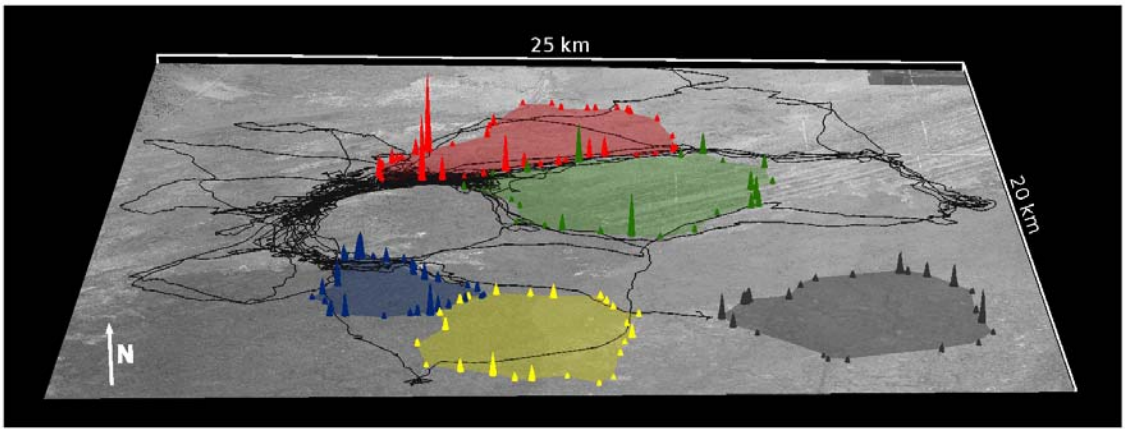

Fig. 5.5. The path from a single non-resident coyote demonstrating how the individual navigates at least five known, and several suspected, coyote territories during the spring and summer of 2005. Cluster-defined boundaries are depicted as cones with frequency of revisitation represented by cone height.

CHAPTER 6

DISCUSSION

The theme of the research presented herein emphasizes the movement and resource selection of two competing predators and their prey, with an interest in the implications of these community processes for mule deer management. In chapter 2, I detailed an approach that takes into consideration the spatial context of aerial coyote removals and my expectation of benefits for mule deer neonate survival. In chapter 3, I utilized hierarchical movement models to evaluate coyote resource selection on a landscape with dynamic and diverse prey resources while balancing risk associated with a more dominant competitor, the cougar. In chapter 4, I evaluated the role of harvest management in cougars, the apex predator within this system, and discuss some of the implications for prey management. Finally, in chapter 5, I presented a novel analytical approach for evaluating site fidelity behavior using animal location technology. Although I demonstrated its use in this chapter with cougar and coyote location data, I applied this same tool to assist with identifying the presence and timing of neonate parturition utilizing location data from pregnant mule deer in chapter 2.

In chapter 2, the primary objective was to highlight an approach for evaluating the spatial match between coyote aerial control and mule deer neonate survival. Winter aerial removal of coyotes is commonly utilized as a management tool for mitigating presumed additive mortality in mule deer neonates during the eight-weeks post-parturition, which may often be a poor presumption. I utilized a multi-level Bayesian model to evaluate the spatial match between aerial removal risk in coyotes relative to my predictions for site

selection in parturient deer during the fawning season. In general, aerial removal operators were extremely effective at targeting coyotes in areas where models predicted a high probability of use during the winter daylight hours, which translated to flat and open shrublands most commonly found at lower elevations. However, two landscape features acted as constraints on an operator's ability to remove a coyote: proximity to tree cover and terrain ruggedness (as measured by the terrain ruggedness index). Coyote susceptibility to removal increased with distance from cover, but declined at higher terrain ruggedness.

When I evaluated spatial overlap between coyote removal risk and deer space use (*i.e.*, weighted congruence), our models indicated no effect of elevation and a strong negative non-linear effect of ruggedness on weighted congruency. This suggests that coyotes occupying flat and open terrain at higher elevations are just as susceptible to removal risk as those at lower elevation. However, declines in overlap were also indicative of differences in expectations of space use in both species, with coyotes generally preferring more open landcover classifications (e.g., barren-ground and shrublands) and mule deer preferring closed habitats (e.g., forest).

I also quantified potential impact at the level of individual removals by simulating home ranges through fitted hidden Markov movement models. Doing so provided an opportunity to generate individual estimates of impact by directly measuring estimated spatial overlap with metrics of interest, in this case relative probability of use by parturient deer. The results demonstrate one of the key points in this assessment, that not all individuals removed are equally impactful on parturient deer space use. Thus, individuals should be weighted according to the degree with which they overlap stated

management objectives rather than included as a raw count, as is often done in predator control studies.

In chapter 3, I implemented a community-based resource selection model with the intent of understanding the space use motivations in coyotes while considering the dynamic nature of an array of prey resources and risk of encountering cougars. To accomplish this task, I integrated several data sources in order to quantify prey availability and risk, including GPS collar data from three different species and survey data for small mammals and lagomorphs. I hypothesized that coyotes would generally select for areas with high lagomorph densities and small mammal biomass over areas favored by parturient deer during the summer months. In addition, I expected coyotes would avoid areas that pose the greatest risk, which was modeled as the relative probability of encountering an active cougar (i.e., intraguild killing) and distance to roads (i.e., anthropogenic risk). The models clearly support the hypotheses and indicate that coyotes are indeed strongly selecting for areas with abundant small prey, particularly lagomorphs, while avoiding areas likely to be risky for coyotes. Interestingly, our marginal estimates indicate coyotes are generally indifferent to areas favored by expectant deer or deer with neonates. However, individual coyotes that occupied home ranges with poorer access to lagomorphs were more likely to select for areas favored by parturient deer. Although this pattern reflects distinct differences in prey-associated cover classes, the opportunistic and generalist tendencies of coyotes hint at an underlying community interaction as a driver of the observed heterogeneity in space use.

In chapter 4, I evaluated cougar movement and resource selection in relation to dynamic movements by two primary prey species, mule deer and elk, and in response to

harvest pressure. The results indicated that cougars largely selected for areas favored by deer throughout much of the year, which is coincident with a majority representation by mule deer within the diet of cougars in this system. However, somewhat surprisingly, there was a complete shift in cougar resource selection towards areas utilized by elk during the harvest (*i.e.,* winter) season. In revisiting the cougar kill data, I documented a concurrent increase in the proportion of elk found within cougar diets during this same period. Cougars were selecting for more rugged terrain during the harvest season, independent of prey movement and resource selection, suggesting this pattern may be a consequence of anthropogenic hunting pressure. As a result, cougars may have limited access to deer that often winter in the surrounding valleys and foothills. Thus, cougars may switch to the more readily available elk occupying higher elevations than that of mule deer. Alternatively, elk may be more susceptible to cougar predation in winter snow pack, suggesting prey switching could be an outcome of reduced handling risk and increased reward for killing larger-bodied prey.

In conclusion, I employed a multi-faceted approach in evaluating the influence of predator control on mule deer populations with an emphasis on the importance of spatial context. First, I demonstrated that the outcomes of aerial coyote control are likely to be highly variable across heterogeneous landscapes at two distinct spatial scales. At larger scales, aerial control is likely to be inconsequential in areas where overlap with parturient deer is low, while potentially more impactful in regions where removal risk is congruent with deer management objectives. Second, I highlighted resource utilization in coyotes in an effort distinguish real from perceived roles attributed to coyotes within this system. Local anecdotes often prescribe wolf-like prey selection tendencies to coyotes, which are

regularly scapegoated for perceived declines in mule deer populations. Yet, my results indicated that coyotes in southcentral Utah are not unique and similar to coyotes from other representative western systems; canids primarily selected for areas that supported robust lagomorph and small mammal populations. However, as coyotes are opportunistic by nature, I further demonstrated that coyotes are increasingly likely to select for areas with a higher probability of encountering parturient deer as lagomorph densities decline at the home range level, which may reflect density-dependent prey switching in coyotes. In addition, I provided some evidence that cougars may regulate coyote access to mule deer from June through August when neonates are most susceptible to coyote predation. And third, I demonstrated a small shift in cougar prey selection may reflect altered space use patterns in response to cougar harvest pressure during the winter. Although the causal nature of these patterns is yet unknown, it could indicate that harvest pressure may release mule deer from some cougar predation during a difficult period of the year for many ungulates. Yet, it is difficult to know to what extent elk influence cougar population sizes, which may have negative consequences for mule deer as a result of apparent competition.

These general conclusions demonstrate that predator-prey processes are not simply one dimensional and that the demographic processes of a focal population are likely the composite outcome of diverse community-level interactions across two or more trophic levels. Moving forward, managers will need to acknowledge that complexity within systems is likely to have important implications for the way we manage specific species. At the very least, we should acknowledge the constraints acting on aerial control of coyotes and limit its use to circumstances where efficiency is maximized, particularly

within the context of the broader community. The approach presented here provides an objective means of performing just such a task by identifying units that are most conducive to coyote aerial removal and most likely be effective in terms of overlap with mule deer fawning sites. Control measures can then be employed in areas with low cougar densities or when lagomorphs have declined below some threshold, provided compensatory immigration is not sufficient to offset population reductions and that removals are sufficiently disruptive to reduce the number of reproductive packs on the landscape. Finally, I quantified the potential impact of individual removals in such a way that the next logical step will be to assess ungulate neonate survival in a spatially explicit context. Given the range of estimates for over 150 removals, I anticipate ignoring important spatial variation regarding the location of the removal will likely bias our ability to accurately evaluate the efficacy of predator control programs.

In light of my findings, we should not expect a strong effect of coyote control on deer populations in Utah given the community (ecology) dynamics of the broader system. However, an obvious next step would be to evaluate the economics of predator control where managers estimate a mean dollar value, along with an associated measure of uncertainty, for each unit increase in the deer population. While there is a strong ethical divide between those that are for or against predator control, evaluating predator control with regards to the financial costs may provide a means of bridging the gap. My recommendation is that this evaluation considers all forms of predator management implemented by a given agency (*e.g.*, aerial control and statewide bounty programs). Doing so will provide transparency and allow for rigorous debate among stakeholders on the objectives and scientific merits of a given predator strategy given the economic costs.

Then, provided predator management is scientifically robust and socially acceptable, both in terms of the ethical debate and the economic costs, agencies can move forward with effective management strategy.

APPENDICES

APPENDIX A. CHAPTER 2 APPENDICES

A-I. RSTAN CODE FOR IMPLEMENTING THE MODEL

```
data {
  // Coyote 3rd Order space use data
  int<lower=0> Nc;                    // number of space use records
  int<lower=1> Ic;                    // number of individuals (for random effect)
  int<lower=1> Kc;                    // number of predictors (fixed effects)
  int<lower=0, upper=1> y_c[Nc];        // Response
  int<lower=1, upper=Ic> indsCoy[Nc];    // The individuals
  matrix[Nc,Kc] xC;                   // Predictors

  // Coyote removal data
  int<lower=0> Nr;                    // number of removal records
  int<lower=1> Na;                    // number of study areas (for random effect)
  int<lower=1> Kr;                    // number of predictors (fixed effects)
  int<lower=0, upper=1> y_r[Nr];        // Response
  int<lower=1,upper=Na> areas[Nr];      // Study Area (north) effect (must be sequential
starting from 1)
  matrix[Nr,Kr] xR;                   // Predictors
  matrix[Nr,Kc] xInt;                 // Predictors for intermediate dataset used in estimating
coyote use

  // Deer 2nd Order space use data
  int<lower=0> Nd;                    // number of space use records
  int<lower=1> Yd;                    // number of years (for random effect)
  int<lower=1> Kd;                    // number of predictors (fixed effects)
  int<lower=0, upper=1> y_d[Nd];        // Response
  int<lower=1,upper=Yd> yearsDeer[Nd];   // The years (must be sequential starting from
1)
  matrix[Nd,Kd] xD;                   // Predictors

  // Penalized regression splines (GAM)
  int<lower=1> N_GAMdat;              // Data (size) subset for model predictions and fit using
GAM
  int<lower=1> N_knots;               // number of knots, penalized regression / thin-plate
  row_vector[N_knots] knots;          // Knot locations, used for subtraction later
  matrix[N_knots, N_knots] knotMat;      // SVD solved matrix on knot locations, used for
design matrix, Z
  matrix[N_GAMdat, Kc] xCoyPred;        // Predictors for Deer extrapolation
  matrix[N_GAMdat, Kd] xDeerPred;       // Predictors for Deer extrapolation
  matrix[N_GAMdat, Kr] xRemPred;        // Predictors for Removal extrapolation

  // GAM prediction
```

```
  int<lower=1> N_GAMpred;              // number of records for GAM prediction
  vector[N_GAMpred] x_GAMpred;         // Predictors for Removal extrapolation
  matrix[N_GAMpred, N_knots] z_GAMpred;   // Predictors for Removal extrapolation
}
parameters {
  // Params for the Coyote space use model
  real<lower=0> sigma_alphaCoyInd;
  real mu_alphaCoyInd;

  // Params for the removal model
  vector[Na] alphaRemArea;        // random intercept, study area
  vector[Kr] betaR;               // beta coeffs for removal model
  real beta] alphaCoyYear;        // random intercept, year
  vector[Ic] alphaCoyInd;         // random intercept, individuals
  vector[Kc] betaCoy;             // beta coeffs for space use model
  real<lower=0> sigma_alphaRemArea;
  real mu_alphaRemArea;

  // Params for the Deer space use model
  vector[Yd] alphaDeerYear;       // random intercept, year
  vector[Kd] betaDeer;            // beta coeffs for space use model
  real<lower=0> sigma_alphaDeerYear;
  real mu_alphaDeerYear;

}
transformed parameters {
  vector<lower=0, upper=1>[Nr] xCoyUse;

  // Estimate Coyote use for removal data
  for (nr in 1:Nr)
    xCoyUse[nr] = inv_logit(mu_alphaCoyInd + xInt[nr]*betaCoy);
}
model {
  vector[Nc] y_c_hat;
  vector[Nr] y_r_hat;
  vector[Nd] y_d_hat;

  // Hyperpriors for space use model
  sigma_alphaCoyInd ~ cauchy(0, 2.5);
  mu_alphaCoyInd ~ normal(0, 10);
  sigma_alphaDeerYear ~ cauchy(0, 2.5);
  mu_alphaDeerYear ~ normal(0, 10);

  // Priors for space use models
  alphaCoyInd ~ normal(mu_alphaCoyInd, sigma_alphaCoyInd);
  betaCoy ~ normal(0, 5);
  alphaDeerYear ~ normal(mu_alphaDeerYear, sigma_alphaDeerYear);
  betaDeer ~ normal(0, 5);
```

```
  // Likelihood for space use models
    // Estimate y_hat for Coyote space use model
  for (nc in 1:Nc)
    y_c_hat[nc] = alphaCoyInd[indsCoy[nc]];
  y_c_hat = y_c_hat + xC*betaCoy;
  y_c ~ bernoulli_logit(y_c_hat);

    // Estimate y_hat for Deer space use model
  for (nd in 1:Nd)
    y_d_hat[nd] = alphaDeerYear[yearsDeer[nd]];
  y_d_hat = y_d_hat + xD*betaDeer;
  y_d ~ bernoulli_logit(y_d_hat);

  // Hyperpriors for space use model
  sigma_alphaRemArea ~ cauchy(0, 2.5);
  mu_alphaRemArea ~ normal(0, 10);

  // Priors for space use model
  alphaRemArea ~ normal(mu_alphaRemArea, sigma_alphaRemArea);
  betaR ~ normal(0, 5);
  betaCoyUse ~ normal(0, 5);

  // Likelihood for removal model
    // Estimate y_hat for removal model
  for (nr in 1:Nr)
    y_r_hat[nr] = alphaRemArea[areas[nr]];
  y_r_hat = y_r_hat + xR*betaR + xCoyUse*betaCoyUse;
  y_r ~ bernoulli_logit(y_r_hat);
}
generated quantities{
  //vector[N_GAMdat] x_CoyUsePred;
  //vector[N_GAMdat] x_RemPred;
  //vector[N_GAMdat] y_DeerPred;
  vector[Nc] y_predC;
  vector[Nr] y_predR;
  vector[Nd] y_predD;

  for (nc in 1:Nc)
    y_predC[nc] = bernoulli_rng(inv_logit(alphaCoyInd[indsCoy[nc]] + xC[nc]*betaCoy));

  for (nr in 1:Nr)
    y_predR[nr] = bernoulli_rng(inv_logit(alphaRemArea[areas[nr]] + xR[nr]*betaR +
xCoyUse[nr]*betaCoyUse));

  for (nd in 1:Nd)
    y_predD[nd] = bernoulli_rng(inv_logit(alphaDeerYear[yearsDeer[nd]] +
xD[nd]*betaDeer));
```

```
  //for (nd in 1:N_GAMdat)
  //  x_CoyUsePred[nd] = inv_logit(mu_alphaCoyInd + xCoyPred[nd]*betaCoy);
  //x_RemPred = mu_alphaRemArea + xRemPred*betaR + x_CoyUsePred*betaCoyUse;
  //y_DeerPred = mu_alphaDeerYear + xDeerPred*betaDeer;
}
```

CHAPTER 2 SUPPLEMENTARY TABLES AND FIGURES

Table A1. A list of model-specific covariates and data sources, as well as the reclassification schemes for all land cover variables (*i.e.*, Landfire 2012).

		Model Inclusion		
Covariate Name	**Source**	**Deer**	**Coyote**	**Removal**
Tertiary Roads	Utah AGRC; http://gis.utah.gov/	Y	Y	N
Dist. to Water	Utah AGRC; http://gis.utah.gov/	Y	Y	N
Max NDVI	NASA (Grant #NNH10ZDA001N, 2011-2014), eMODIS NDVI (2015); http://earthexplorer.usgs.gov/	Y	N	N
Elevation	USGS DEM (10m) – Utah AGRC; http://gis.utah.gov/	N	N	N
Ruggedness, TRI	Derived from DEM; R package raster, ?terrain()	N	N	Y
Ruggedness, VRM	Derived from DEM; following Sappington et al. (2007)	Y	Y	N
Aspect	Derived from DEM	Y	Y	Y
Prob. Of Use by Coyotes	Derived from coyote resource selection model	N	N	Y
Landfire 2012	EVT & EVC; http://landfire.gov			
EVT: Shrub	Value = 3064,3066,3079,3080:3082,3086,3093,3103,3104, 3107,3108,3124:3127,3153,3210,3211,3214,3217,3220,3904, 3914,3923,3928,3943	Y	Y	N
EVT: Grass	Value = 3070,3135,3143:3146,3181:3183,3903,3924,3929, 3944	Y	Y	N
EVT: Aspen	Value = 3011	Y	Y	N
EVT: PJ	Value = 3016,3019,3049,3115	Y	Y	N
EVT: Conifer	Value = 3050:3052,3054:3057,3117,3208,3901,3921,3941	Y	Y	N
EVT: Mixed	Value = 3061,3902,3922,3942	Y	Y	N
EVT: HW	Value = 3012,3062,3154,3159,3164,3180,3251,3252,3259, 3900,3920,3940	Y	Y	N
EVT: Barren	Value = 3001,3006,3218,3219,3222,3294	N	Y	N
EVC: Tree Cover	>50%	N	N	Y

Table A2. Model selection output for coyote resource selection. The 'd*' indicates a 'distance to' covariate and the (2) represents a second order polynomial for the preceding variable. HW represents non-aspen hardwood, PJ represents 'pinyon-juniper', Mix represents mixed conifer and hardwood, and VRM is the vector ruggedness metric. LOOic is the leave-one-out cross-validation information criterion and K is the estimated number of parameters in the model. All models incorporated a random effect of individual.

Model	Coefficients	LOOic	ΔLOOic	K
1	dConifer + dMix + dHW(2) + dShrub + dGrass(2) + dBarren + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18963.82	0.00	23.46
2	dConifer + dMix + dHW(2) + dPJ(2) + dShrub + dGrass(2) + dBarren + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18964.97	1.15	25.59
3	dConifer(2) + dMix + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18965.29	1.48	27.79
4	dConifer(2) + dMix + dHW(2) + dShrub + dGrass(2) + dBarren + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18965.38	1.56	24.54
5	dConifer(2) + dMix + dHW(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18965.73	1.91	26.42
6	dConifer(2) + dMix + dHW(2) + dShrub + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18966.85	3.03	25.23
7	dConifer + dMix + dHW(2) + dPJ(2) + dShrub + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18967.02	3.21	26.55
8	dConifer(2) + dMix + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18967.06	3.25	28.66
9	dConifer(2) + dMix(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18967.80	3.98	29.11
10	dConifer(2) + dMix + dHW(2) + dPJ(2) + dShrub + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18968.27	4.45	27.52
11	dConifer(2) + dMix(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM + dRoads + dWater(2) + E + S + W + NoAsp	18982.58	18.76	29.02
12	dConifer(2) + dMix(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM + dRoads(2) + dWater + E + S + W + NoAsp	18982.63	18.82	28.04
13	dConifer(2) + dMix(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dBarren(2) + VRM(2) + dRoads(2) + dWater + E + S + W + NoAsp	18983.38	19.56	28.95
14	dConifer + dMix + dHW(2) + dGrass + dBarren + VRM + dRoads + dWater + E + S + W + NoAsp	19002.02	38.20	20.86
15	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + VRM + dRoads + dWater + E + S + W + NoAsp	19004.06	40.25	21.73
16	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + dWater + E + S + W + NoAsp	19012.41	48.59	19.63
17	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + dRoads + dWater + E + S + W + NoAsp	19012.70	48.88	20.55
18	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + dRoads + E + S + W + NoAsp	19034.97	71.15	19.56
19	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + E + S + W + NoAsp	19035.65	71.83	18.78

Table A2. cont.

20	VRM + dRoads + dWater + E + S + W + NoAsp	19105.68	141.86	15.32
21	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + VRM + dRoads + dWater	19107.03	143.21	17.76
22	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + dWater	19115.43	151.62	15.70
23	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + VRM + dRoads	19130.65	166.83	16.46
24	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + VRM	19131.16	167.34	15.69
25	dConifer + dMix + dHW + dPJ + dShrub + dGrass + dBarren + dRoads	19141.36	177.54	15.66
26	Null Fixed	19246.90	283.08	8.29

Table A3. Model selection output for coyote removal (*i.e.*, risk) model. The 'dTreeCover' represents distance to 50% tree cover and the (2) indicates a second order polynomial for the preceding variable. TRI is the terrain ruggedness index. LOOic is the leave-one-out cross-validation information criterion and K is the estimated number of parameters in the model. All models incorporated a random effect of area.

Model	Coefficients	LOOic	ΔLOOic	K
1	CoyUse + S + E + dTreeCover(2) + TRI(2)	1928.73	0.00	8.68
2	CoyUse + S + E + dTreeCover + TRI(2)	1935.14	6.41	7.84
3	CoyUse + S + E + dTreeCover(2) + TRI	1939.54	10.81	7.57
4	CoyUse	1944.12	15.39	3.59
5	CoyUse + S + E + dTreeCover + TRI	1945.77	17.03	6.43
6	CoyUse + S + E	1948.47	19.74	5.98
7	Null Fixed	1957.51	28.78	1.93

Table A4. Model selection output for deer resource selection. The 'd*' indicates a 'distance to' covariate and the (2) represents a second order polynomial for the preceding variable. HW represents non-aspen hardwood, PJ represents 'pinyon-juniper', Mix represents mixed conifer and hardwood, and VRM is the vector ruggedness metric. LOOic is the leave-one-out cross-validation information criterion and K is the estimated number of parameters in the model. All models incorporated a random effect of year.

Model	Coefficients	LOOic	ΔLOOic	K
1	dRoads(2) + NDVI(2) + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	70003.49	0.00	23.93
2	dRoads + NDVI(2) + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	70103.75	100.26	23.48
3	dRoads + NDVI(2) + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	70589.71	586.22	21.64
4	dRoads + NDVI(2) + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	71892.77	1889.28	17.23
5	dRoads + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	73838.49	3835.00	20.77
6	dRoads(2) + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW()2 + dSprings + E + S + W + NoAsp	74669.76	4666.28	21.15
7	dRoads + NDVI + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	74787.01	4783.52	21.55
8	dRoads + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	74790.79	4787.30	20.27
9	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings(2) + E + S + W + NoAsp	74935.23	4931.74	17.73
10	DRoads(2) + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75772.99	5769.50	17.71
11	dRoads + NDVI + VRM(2) + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75859.48	5855.99	17.16
12	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75863.39	5859.90	16.40
13	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	76969.25	6965.76	15.94
14	dRoads + NDVI + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	76993.37	6989.88	15.21
15	NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77050.25	7046.76	15.03
16	NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77050.25	7046.76	15.03

Table A4. cont.

17	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77147.97	7144.49	12.58
18	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings	77323.36	7319.88	9.36
19	NDVI + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78017.03	8013.54	9.81
20	dRoads + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78035.02	8031.54	9.92
21	VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78058.18	8054.69	9.91
22	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78094.50	8091.01	9.26
23	Null Fixed	89287.99	19284.51	3.54

Table A5. The estimated median and coefficient of variation (CV) in overlap of individual coyotes with relative probability of use by parturient deer. Larger median estimates indicate greater potential impact on mule deer populations. Larger CVs indicates more spatial heterogeneity in overlap at the home range level. HPDI is a highest posterior density interval estimate.

		Median			Coefficient of Variation		
Point ID	***Study Area***	***Estimate***	***Lower HPDI***	***Upper HPDI***	***Estimate***	***Lower HPDI***	***Upper HPDI***
R1_2012	N	0.165	0	0.496	111.012	62.794	218.419
R2_2012	N	0.182	0	0.567	107.435	56.907	201.816
R3_2012	N	0.192	0	0.583	105.205	57.107	198.074
R4_2012	N	0.191	0	0.590	106.217	63.495	209.506
R5_2012	N	0.184	0	0.480	106.278	61.436	199.678
R6_2012	N	0.191	0	0.461	105.053	66.000	196.261
R7_2012	N	0.143	0	0.375	119.645	66.264	259.743
R8_2012	N	0.137	0	0.386	120.352	63.904	318.111
R9_2012	N	0.145	0	0.341	120.955	76.243	286.537
R10_2012	N	0.139	0	0.330	123.508	68.621	268.174
R11_2012	N	0.028	0	0.471	168.242	64.265	650.518
R12_2012	N	0.000	0	0.162	241.436	73.989	1561.062
R13_2012	N	0.176	0	0.770	112.662	52.291	287.130
R14_2012	N	0.231	0	0.770	107.483	50.847	252.280
R15_2012	N	0.498	0	1.106	108.839	53.192	278.074
R16_2012	N	0.387	0	0.807	101.306	54.002	224.191
R17_2012	N	0.402	0	0.743	98.265	49.193	209.184
R18_2012	N	0.109	0	0.608	130.935	56.430	383.588
R19_2012	N	0.164	0	0.629	124.639	54.935	370.635
R20_2012	N	0.346	0	0.840	106.988	59.561	269.720
R21_2012	N	0.403	0	0.891	103.326	57.941	229.928
R22_2012	N	0.415	0	0.862	102.763	57.822	228.661
R23_2012	N	0.401	0	0.842	102.184	51.549	200.754
R24_2012	N	0.448	0	1.048	111.061	49.332	424.418
R25_2012	N	0.352	0	1.056	115.352	51.288	548.719
R26_2012	N	0.400	0	1.032	113.637	44.027	620.718
R26.1_2012	S	0.000	0	0.618	172.234	44.265	1084.345
R26.2_2012	S	0.058	0	0.560	134.146	55.642	494.614
R30_2012	N	0.242	0	0.781	104.700	46.291	264.541

Table A5. cont.

R31_2012	N	0.264	0	0.772	98.978	52.633	196.259
R32_2012	N	0.248	0	0.764	102.357	50.717	211.169
R33_2012	N	0.481	0	0.944	98.843	55.395	187.745
R34_2012	N	0.372	0	0.849	106.742	59.026	286.123
R35_2012	N	0.515	0	1.109	101.960	51.909	202.366
R36_2012	N	0.447	0	1.040	109.153	49.763	429.985
R37_2012	N	0.274	0	0.989	117.156	50.916	596.210
R38_2012	N	0.407	0	0.942	109.526	45.944	388.127
R39_2012	N	0.235	0	0.850	116.311	48.130	560.564
R40_2012	N	0.216	0	0.865	117.029	45.177	556.514
R41_2012	N	0.275	0	0.682	93.819	52.723	161.752
R42_2012	N	0.406	0	0.805	88.079	49.060	154.598
R43_2012	N	0.385	0	0.789	89.228	49.873	150.263
R44_2012	N	0.293	0	0.704	93.089	51.676	159.928
R45_2012	N	0.310	0	0.697	92.010	52.628	147.697
R46_2012	N	0.213	0	0.565	106.954	57.154	243.604
R47_2012	N	0.232	0	0.557	104.251	59.490	242.024
R48_2012	N	0.132	0	0.431	127.233	69.649	320.620
R1_2013	N	0.153	0	0.395	117.324	70.275	254.997
R2_2013	N	0.162	0	0.375	112.350	69.525	232.572
R3_2013	N	0.145	0	0.346	121.225	71.683	268.299
R4_2013	N	0.407	0	0.837	98.901	45.970	226.318
R5_2013	N	0.389	0	0.889	100.787	47.708	224.198
R6_2013	N	0.377	0	0.827	95.604	44.489	204.981
R7_2013	N	0.099	0	0.693	131.541	48.601	704.582
R8_2013	N	0.492	0	1.044	107.452	51.747	333.556
R9_2013	N	0.548	0	1.141	104.736	49.908	259.580
R10_2013	N	0.574	0	1.112	101.014	53.173	182.902
R11_2013	N	0.570	0	1.123	101.869	55.950	193.734
R12_2013	N	0.504	0	1.071	105.161	49.470	303.648
R13_2013	N	0.452	0	1.056	106.762	54.943	297.946
R14_2013	N	0.452	0	1.058	107.174	48.811	337.979
R15_2013	N	0.455	0	0.861	98.192	46.456	223.475

Table A5. cont.

R16_2013	N	0.553	0	1.050	95.124	48.387	196.185
R17_2013	N	0.486	0	1.040	102.350	53.214	203.170
R18_2013	N	0.235	0	0.694	117.084	56.476	335.208
R19_2013	N	0.246	0	0.702	113.732	59.147	324.970
R22_2013	N	0.106	0	0.679	130.151	49.112	421.884
R23_2013	N	0.559	0	1.075	102.255	53.708	204.958
R24_2013	N	0.396	0	0.983	105.756	55.912	396.456
R25_2013	N	0.000	0	0.244	185.758	74.961	815.850
R26_2013	N	0.130	0	0.515	118.539	67.147	300.463
R27_2013	N	0.144	0	0.591	116.479	58.882	259.052
R28_2013	N	0.036	0	0.455	163.169	65.285	629.659
R29_2013	N	0.024	0	0.239	177.084	78.154	685.559
R30_2013	N	0.023	0	0.256	177.267	64.858	633.239
R31_2013	N	0.001	0	0.204	207.906	77.259	1020.768
R32_2013	N	0.000	0	0.655	157.513	52.574	1443.559
R33_2013	N	0.000	0	0.643	154.839	59.159	996.434
R34_2013	N	0.493	0	1.009	98.673	55.991	167.329
R1_2014	S	0.306	0	0.756	103.676	41.370	242.892
R2_2014	S	0.012	0	0.549	164.461	43.486	816.458
R3_2014	S	0.304	0	0.602	102.955	58.343	241.675
R5_2014	S	0.074	0	0.551	133.787	62.488	284.827
R6_2014	S	0.076	0	0.555	140.526	58.620	375.003
R7_2014	S	0.107	0	0.563	133.486	53.497	371.641
R8_2014	S	0.185	0	0.541	122.171	57.458	337.858
R10_2014	S	0.304	0	0.741	103.780	40.264	291.515
R11_2014	S	0.352	0	0.754	95.892	42.290	257.278
R12_2014	S	0.361	0	0.723	95.013	48.227	239.340
R13_2014	S	0.306	0	0.613	104.103	55.981	268.425
R14_2014	S	0.294	0	0.590	105.105	53.229	297.091
R15_2014	S	0.030	0	0.545	158.700	55.548	358.562
R16_2014	S	0.047	0	0.550	146.780	52.879	348.065
R17_2014	S	0.152	0	0.580	129.252	56.879	294.861
R18_2014	S	0.364	0	0.748	95.428	42.878	269.309

Table A5. cont.

R19_2014	S	0.002	0	0.286	261.381	69.279	643.799
R20_2014	S	0.001	0	0.275	274.853	67.044	765.153
R21_2014	S	0.001	0	0.291	282.450	79.838	821.449
R22_2014	S	0.019	0	0.412	166.374	74.119	319.437
R23_2014	S	0.000	0	0.700	145.396	45.059	696.973
R24_2014	S	0.287	0	0.722	105.015	42.264	294.626
R25_2014	S	0.091	0	0.712	126.573	39.673	477.641
R26_2014	S	0.118	0	0.599	128.775	52.063	338.586
R27_2014	S	0.100	0	0.587	131.753	54.472	359.068
R28_2014	S	0.173	0	0.602	121.961	52.428	332.455
R29_2014	S	0.283	0	0.747	106.305	37.905	266.450
R30_2014	S	0.361	0	0.720	94.820	45.683	234.249
R31_2014	S	0.364	0	0.735	94.175	46.903	217.557
R32_2014	S	0.286	0	0.759	107.453	42.302	263.308
R33_2014	S	0.306	0	0.779	103.562	40.779	277.916
R34_2014	S	0.276	0	0.758	108.690	39.850	272.920
R35_2014	S	0.004	0	0.387	231.867	68.593	428.762
R36_2014	S	0.000	0	0.233	319.087	63.101	1169.336
R40_2014	S	0.036	0	0.538	154.356	58.750	377.842
R1_2015	S	0.000	0	0.500	203.380	54.981	1411.301
R2_2015	S	0.039	0	0.566	148.713	54.423	776.174
R4_2015	S	0.005	0	0.425	206.604	62.078	464.030
R5_2015	S	0.015	0	0.326	178.852	72.050	426.737
R6_2015	S	0.004	0	0.101	220.762	81.436	611.748
R7_2015	S	0.000	0	0.080	228.056	96.490	690.882
R8_2015	S	0.052	0	0.502	141.363	65.697	260.646
R9_2015	S	0.000	0	0.570	178.754	45.256	831.733
R10_2015	S	0.007	0	0.435	192.465	61.895	452.356
R11_2015	S	0.006	0	0.406	193.054	70.337	464.111
R12_2015	S	0.000	0	0.158	305.439	74.364	1305.843
R13_2015	S	0.002	0	0.496	237.546	54.555	1343.293
R14_2015	S	0.000	0	0.472	215.453	54.888	1224.427
R15_2015	S	0.011	0	0.223	191.096	63.689	475.735

Table A5. cont.

R16_2015	S	0.042	0	0.442	145.643	64.632	253.008
R17_2015	S	0.031	0	0.587	153.927	56.139	371.865
R18_2015	S	0.059	0	0.568	140.260	53.395	726.575
R19_2015	S	0.038	0	0.572	149.104	50.755	774.473
R20_2015	S	0.256	0	0.593	111.376	53.845	248.585
R21_2015	S	0.243	0	0.607	113.282	52.648	239.784
R22_2015	S	0.261	0	0.600	110.643	55.148	229.039
R23_2015	S	0.261	0	0.584	110.895	51.400	240.931
R24_2015	S	0.217	0	0.548	115.086	59.918	333.736
R25_2015	S	0.002	0	0.190	257.610	83.393	558.288
R26_2015	S	0.002	0	0.184	260.086	81.867	613.738
R27_2015	S	0.002	0	0.147	265.088	84.462	779.937
R28_2015	S	0.002	0	0.481	198.853	59.534	1440.797
R29_2015	S	0.039	0	0.514	151.940	55.166	391.249
R30_2015	S	0.056	0	0.491	147.124	61.558	459.812
R31_2015	S	0.000	0	0.315	240.101	71.177	509.273
R32_2015	S	0.150	0	0.605	123.133	50.635	483.286
R33_2015	S	0.001	0	0.379	233.520	68.261	640.783
R34_2015	S	0.011	0	0.496	189.788	61.406	464.678
R35_2015	S	0.010	0	0.491	188.678	59.183	513.246
R36_2015	S	0.100	0	0.504	137.838	56.472	404.236
R37_2015	S	0.118	0	0.520	132.231	60.382	401.434
R38_2015	S	0.053	0	0.541	140.630	61.017	276.896
R39_2015	S	0.000	0	0.540	186.509	49.645	1274.006
R40_2015	S	0.121	0	0.730	125.084	38.780	398.744
R41_2015	S	0.362	0	0.734	94.203	43.889	245.612
R42_2015	S	0.001	0	0.525	176.204	54.543	904.068
R43_2015	S	0.000	0	0.525	206.601	45.609	1232.182

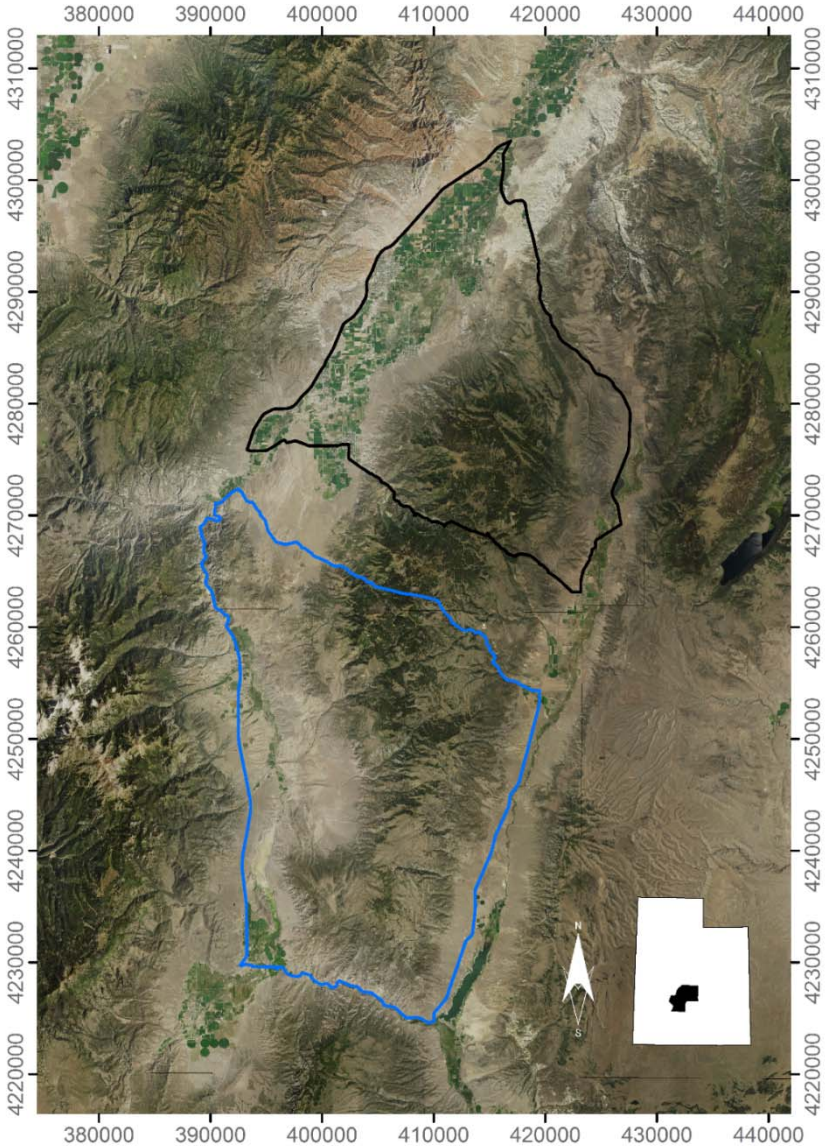

Figure A1. A map of Monroe Mountain and surrounding valleys, a ranger district in Fishlake National Forest, UT. The colored polygons (Black: 2012-2013; Blue: 2014-2015) represent the boundaries provided to Wildlife Services for winter aerial removal of coyotes.

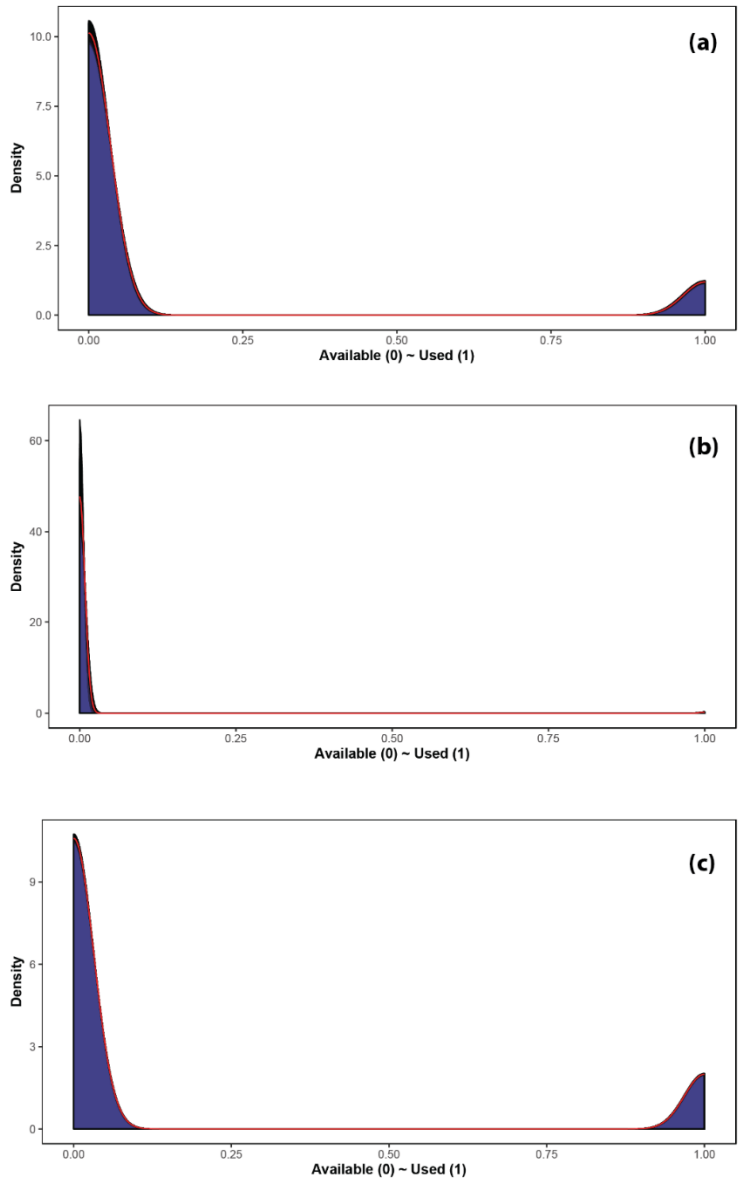

Figure A2. Visual posterior predictive checks for the coyote resource selection (a), coyote removal (b), and deer resource selection (c) models. Density plots show the observed data (red) versus posterior predictions (black bands on top blue densities) for each response variable in the respective models. Although histograms are more appropriate for discrete data (0/1), density plots better demonstrate the strong predictive fit in this case.

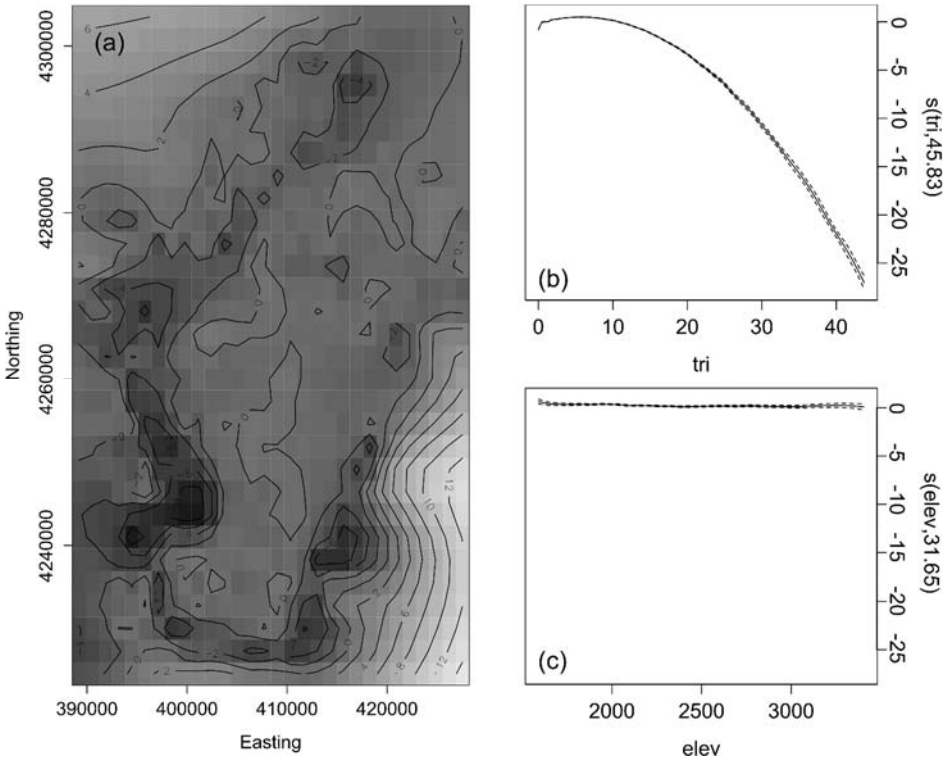

Figure A3. The results from a generalized additive model with median congruence as the response and predictor smooths for spatial coordinates (a), terrain ruggedness index (b, tri) and elevation (c, elev). Numeric values in the smooth labels (y-axes) contain the number of estimated degrees of freedom.

APPENDIX B. CHAPTER 3 APPENDICES

B-I. RSTAN CODE FOR IMPLEMENTING THE OVERALL MODEL

```
## Conditional logistic regression w/random effects
## (the same likelihood calculation as used by survival::clogit in R and
## clogit in Stata)
## Modified from David C Muller original code on stan google group

functions {
 ## function to return the number of observations in a group
 int group_size(int[] ref, int value) {
  int count;
  count = 0;
  for (ii in 1:size(ref))
   if (ref[ii]==value)
    count = count + 1;
   return count;
 }

 ## function to subset a vector (return just those observations in a given group)
 vector subset_vector(vector y, int[] ref, int value) {
  int jj;
  vector[group_size(ref, value)] res;
  if (size(ref) != rows(y))
   reject("illegal input: non-matching dimensions")
  jj = 1;
  for(ii in 1:size(ref)) {
   if (ref[ii] == value) {
    res[jj] = y[ii];
    jj = jj+1;
   }
  }
  return res;
 }

 ## function to subset an integer array (return just those observations in a given group)
 int[] subset_intarray(int[] y, int[] ref, int value) {
  int jj;
  int res[group_size(ref, value)];
  if (size(ref) != size(y))
   reject("illegal input: non-matching dimensions")
  jj = 1;
  for(ii in 1:size(ref)) {
   if (ref[ii] == value) {
```

```
      res[jj] = y[ii];
      jj = jj+1;
    }
  }
  return res;
}

## recursive function to evaluate the denominator of the conditional likelihood
real cl_denom(int N_g, int D_g, vector xb);
real cl_denom(int N_g, int D_g, vector xb) {
  real res;
  if (N_g < D_g) {
    return 0;
  }
  if (D_g == 0) {
    return 1;
  }
  res = cl_denom(N_g-1, D_g, xb) + exp(log(cl_denom(N_g-1, D_g-1, xb)) + xb[N_g]);
  return res;
}
}

data {
// Coyote SSF
int<lower=0> N;                    // Number of observations
int<lower=1> n_grp;                // Number of groups
int<lower=1> n_coef;               // Number of coefficients (log odds ratios) to estimate
int<lower=1, upper=n_grp> grp[N];     // stratum/group identifier
int<lower=0, upper=1> y[N];           // array of 0/1 outcomes
matrix[N, n_coef] xCoy;               // Matrix of regressors
int<lower=0> Ncoy;                 // Number of individuals
int<lower=1, upper=Ncoy> iCoy[N];     // Individual identifier
int<lower=0> Nyear_c;              // Number of coyote years
int<lower=1, upper=Nyear_c> yCoy[N];   // Individual identifier

// Cougar Resource Selection
int<lower=0> Np;                   // number of records
int<lower=1> Nyear_p;              // number of years (for random effect)
int<lower=1> Npuma;                // number of individuals (for random effect)
int<lower=1> Kpuma;                // number of predictors (fixed effects)
int<lower=0, upper=1> y_Puma[Np];      // Response
int<lower=1,upper=Nyear_p> yPuma[Np];   // The years (must be integers starting from 1)
int<lower=1, upper=Npuma> iPuma[Np];    // The individuals (must be integers starting
from 1)
matrix[Np, Kpuma] xPuma;               // Predictors

// Cougar Kill Site Selection
int<lower=0> Nk;                   // number of records
```

```
  int<lower=1> Nyear_k;                // number of years (for random effect)
  int<lower=1> Kkill;                 // number of predictors (fixed effects)
  int<lower=0, upper=1> y_Kill[Nk];     // Response
  int<lower=1,upper=Nyear_k> yKill[Nk];  // The years (must be integers starting from 1)
  matrix[Nk, Kkill] xKill;             // Predictors

  // Deer Fawn Site Selection
  int<lower=0> Nd;                    // number of records
  int<lower=1> Nyear_d;                // number of years (for random effect)
  int<lower=1> Kdeer;                 // number of predictors (fixed effects)
  int<lower=0, upper=1> y_Deer[Nd];     // Response
  int<lower=1,upper=Nyear_d> yDeer[Nd];  // The years (must be integers starting from 1)
  matrix[Nd, Kdeer] xDeer;             // Predictors

  // Data for prediction
  matrix[N, Kpuma] xPumaPred;
  matrix[N, Kkill] xKillPred;
  matrix[N, Kdeer] xDeerPred;
}

transformed data {
  // Coyote SSF
  int n_group[n_grp]; // number of observations in the group
  int n_case[n_grp];  // number of cases/events in the group
  for (ii in 1:n_grp) {
    n_group[ii] = group_size(grp, ii);
    {
      int subset_y[n_group[ii]];
      subset_y = subset_intarray(y, grp, ii);
      n_case[ii] = group_size(subset_y, 1);
    }
  }
}

parameters {
  // Cougar Resource Selection
  vector[Nyear_p] alphaYearPuma;      // random intercept, year
  vector[Npuma] alphaIndPuma;         // random intercept, individuals
  vector[Kpuma] betaPuma;             // beta coeffs
  real<lower=0> sigma_alphaYearPuma;   // hyper-parameters
  real mu_alphaYearPuma;
  real<lower=0> sigma_alphaIndPuma;
  real mu_alphaIndPuma;

  // Cougar Kill Site Selection
  vector[Nyear_k] alphaYearKill;      // random intercept, year
  vector[Kkill] betaKill;             // beta coeffs
  real<lower=0> sigma_alphaYearKill;
```

```
  real mu_alphaYearKill;

  // Deer Fawn Site Selection
  vector[Nyear_d] alphaYearDeer;      // random intercept, year
  vector[Kdeer] betaDeer;             // betaDeer coeffs
  real<lower=0> sigma_alphaYearDeer;
  real mu_alphaYearDeer;

  // Coyote SSF FE and RE
  vector[n_coef] betaCoy;
  vector[Ncoy] gIndCoy;
  vector[Nyear_c] gYearCoy;
  real<lower=0> sigma_IndCoy;
  real<lower=0> sigma_YearCoy;
  real mu_IndCoy;
  real mu_YearCoy;

  // Coefficients in SSF for predicted data
  vector[3] betaPred;
}

//transformed parameters {
//  vector[n_coef] oddsratio;

//  # Output Odds Ratios
//  oddsratio = exp(betaCoy);
//}

model {

  // Local variables for predicted data
  vector[N] pxPumaPred;
  vector[N] pxKillPred;
  vector[N] pxDeerPred;
  vector[Np] y_Puma_hat;
  vector[Nk] y_Kill_hat;
  vector[Nd] y_Deer_hat;
  vector[N] xb; # observation level linear predictor
  real ll; # log likelihood
  int pos; # incrementing index

  // Priors for the coefficients for predicted data
  betaPred ~ normal(0, 1);

  // Cougar Resource Selection
  // Hyperpriors
  sigma_alphaYearPuma ~ cauchy(0, 2.5);
  mu_alphaYearPuma ~ normal(0, 5);
```

```
sigma_alphaIndPuma ~ cauchy(0, 2.5);
mu_alphaIndPuma ~ normal(0, 5);

// Priors
alphaYearPuma ~ normal(mu_alphaYearPuma, sigma_alphaYearPuma);
alphaIndPuma ~ normal(mu_alphaIndPuma, sigma_alphaIndPuma);
betaPuma ~ normal(0, 1);

// Likelihood
for (n in 1:Np)
  y_Puma_hat[n] = alphaYearPuma[yPuma[n]] + alphaIndPuma[iPuma[n]];
y_Puma_hat = y_Puma_hat + xPuma*betaPuma;
y_Puma ~ bernoulli_logit(y_Puma_hat);


// Cougar Kill Site Selection
// Hyperpriors
sigma_alphaYearKill ~ cauchy(0, 2.5);
mu_alphaYearKill ~ normal(0, 10);

// Priors
alphaYearKill ~ normal(mu_alphaYearKill, sigma_alphaYearKill);
betaKill ~ normal(0, 1);

// Likelihood
for (n in 1:Nk)
  y_Kill_hat[n] = alphaYearKill[yKill[n]];
y_Kill_hat = y_Kill_hat + xKill*betaKill;
y_Kill ~ bernoulli_logit(y_Kill_hat);


// Deer Fawn Site Selection
// Hyperpriors
sigma_alphaYearDeer ~ cauchy(0, 2.5);
mu_alphaYearDeer ~ normal(0, 10);

// Priors
alphaYearDeer ~ normal(mu_alphaYearDeer, sigma_alphaYearDeer);
betaDeer ~ normal(0, 1);

// Likelihood
for (n in 1:Nd)
  y_Deer_hat[n] = alphaYearDeer[yDeer[n]];// + alphaIndDeer[iDeer[n]];
y_Deer_hat = y_Deer_hat + xDeer*betaDeer;
y_Deer ~ bernoulli_logit(y_Deer_hat);


// Predicting new data for SSF
```

```
  for (nd in 1:N) {
    pxPumaPred[nd] = inv_logit(mu_alphaIndPuma + mu_alphaYearPuma +
xPumaPred[nd]*betaPuma);
    pxKillPred[nd] = inv_logit(mu_alphaYearKill + xKillPred[nd]*betaKill);
    pxDeerPred[nd] = inv_logit(mu_alphaYearDeer + xDeerPred[nd]*betaDeer);
  }

  // Coyote SSF
  // Priors for Coyote SSF
  mu_IndCoy ~ normal(0, 5);
  mu_YearCoy ~ normal(0, 5);
  sigma_IndCoy ~ cauchy(0, 2.5);
  sigma_YearCoy ~ cauchy(0, 2.5);
  gIndCoy ~ normal(mu_IndCoy, sigma_IndCoy);
  gYearCoy ~ normal(mu_YearCoy, sigma_YearCoy);

  // diffuse normal prior for log odds ratios
  betaCoy ~ normal(0, 3);

  // log likelihood is a sum over each group
  for (n in 1:N)
    xb[n] = xCoy[n] * betaCoy +
          pxPumaPred[n] * betaPred[1] +
          pxKillPred[n] * betaPred[2] +
          pxDeerPred[n] * betaPred[3] +
          gIndCoy[iCoy[n]] + gYearCoy[yCoy[n]];

  pos = 1;
  for (ii in 1:n_grp) {
    int y_g[n_group[ii]];
    vector[n_group[ii]] xb_g;
    y_g = segment(y, pos, n_group[ii]);
    xb_g = segment(xb, pos, n_group[ii]);
    ll = dot_product(to_vector(y_g), xb_g) - log(cl_denom(n_group[ii], n_case[ii], xb_g));
    target += ll;
    pos = pos + n_group[ii];
  }
}
```

CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES

Table B1. All remote-sensing derived variables, their sources, and the models in which they were used.

Covariate Name	Source	Cougar	Cougar Cache	Deer	Coyote	Lagomorphs	Small Mammals
Tertiary Roads	Utah AGRC; http://gis.utah.gov/	Y	Y	Y	Y	N	N
Dist. to Water	Utah AGRC; http://gis.utah.gov/	Y	Y	Y	N	N	N
Max NDVI	NASA (Grant #NNH10ZDA001N, 2011-2014)	N	N	Y	N	N	N
Elevation	USGS DEM (10m) – Utah AGRC; http://gis.utah.gov/	N	Y	N	N	Y	Y
Ruggedness, VRM	Derived from DEM; following Sappington et al. (2007)	Y	Y	Y	N	N	N
Aspect	Derived from DEM	Y	N	Y	N	N	N
Slope	Derived from DEM	N	Y	N	N	N	N
Landfire 2012	EVT & EVC; http://landfire.gov						
EVT: Shrub	Value = 3064,3066,3079,3080:3082,3086,3093,3103,3104, 3107,3108,3124:3127,3153,3210,3211,3214,3217,3220,3904, 3914,3923,3928,3943	Y	N	Y	N	N	N
EVT: Grass	Value = 3070,3135,3143:3146,3181:3183,3903,3924,3929, 3944	Y	N	Y	N	N	N
EVT: Aspen	Value = 3011	Y	N	Y	N	N	N
EVT: PJ	Value = 3016,3019,3049,3115	Y	N	Y	N	N	N
EVT: Conifer	Value = 3050:3052,3054:3057,3117,3208,3901,3921,3941	Y	N	Y	N	N	N
EVT: Mixed	Value = 3061,3902,3922,3942	N	N	N	N	N	N

Table B1. cont.

EVT: HW	Value = 3012,3062,3154,3159,3164,3180,3251,3252,3259, 3900,3920,3940	Y	Y	Y	N	N	N
EVT: Barren	Value = 3001,3006,3218,3219,3222,3294	Y	Y	N	N	N	N
EVC: Tree Cover	>50%	N	Y	N	N	Y	Y

Table B2. All small mammal species that were captured during surveys and included in our biomass index for the coyote space use model. Species group identifies group membership used to permit robust estimation of capture probabilities and population abundance.

Common Name	Species Name	Species Group	Mean Mass (g)
Least Chipmunk	*Neotamias minimus*	Chipmunks	49
Uinta Chipmunk	*Neotamias umbrinus*	Chipmunks	49
Cliff Chipmunk	*Neotamias dorsalis*	Chipmunks	49
Deer Mouse	*Peromyscus maniculatus*	Mice	28.5
Pinyon Mouse	*Peromyscus truei*	Mice	28.5
Merriam's Shrew	*Sorex merriami*	Mice	28.5
Great Basin Pocket Mouse	*Perognathus pervus*	Mice	28.5
Bushy-tailed woodrat	*Neotoma cinerea*	Rats	145
Desert Woodrat	*Neotoma lepida*	Rats	145
Golden Mantled Ground Squirrel	*Spermophilus lateralis*	Squirrels	453.75
Rock Squirrel	*Spermophilus variegatus*	Squirrels	453.75
Southern Red-backed Vole	*Myodes gapperi*	Voles	45
Sagebrush Vole	*Lemmiscus curtatus*	Voles	45
Montane Vole	*Microtus montanus*	Voles	45

Table B3. Model selection output for the cougar resource selection model (3rd order). Models are ranked by the estimated leave-one-out information criterion. PJ stands for pinyon and juniper cover, HW for hardwood cover, and VRM for the vector ruggedness metric. Coefficients with preceding 'd' indicate a distance-based metric and those followed by (2) indicate a second order polynomial.

Model	Coefficients	LOOic	ΔLOOic	K
1	dAspen(2) + dConifer(2) + dHW(2) + dPJ(2) + dGrass(2) + dRock(2) + VRM(2) + dRoads(2) + dSprings(2) + West	13443.94	0.00	30.98
2	dAspen(2) + dConifer(2) + dHW(2) + dPJ(2) + dGrass(2) + dRock + VRM(2) + dRoads(2) + dSprings(2) + West	13448.91	4.97	30.01
3	dAspen(2) + dConifer(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dRock(2) + VRM(2) + dRoads(2) + dSprings(2) + East + South + West	13451.29	7.35	35.12
4	dAspen(2) + dConifer + dHW(2) + dPJ + dGrass(2) + dRock + VRM(2) + dRoads(2) + dSprings + West	13457.16	13.22	26.92
5	dAspen(2) + dConifer + dHW(2) + dPJ + dGrass(2) + dRock + VRM(2) + dRoads(2) + dSprings + West	13457.16	13.22	26.92
6	dAspen(2) + dConifer(2) + dHW(2) + dPJ + dGrass(2) + dRock + VRM(2) + dRoads(2) + dSprings + West	13457.99	14.04	28.06
7	dAspen(2) + dConifer + dHW(2) + dPJ(2) + dGrass(2) + dRock(2) + VRM(2) + dRoads(2) + dSprings + West	13458.45	14.51	28.05
8	dAspen(2) + dConifer(2) + dHW(2) + dPJ(2) + dGrass(2) + dRock + VRM(2) + dRoads(2) + dSprings + West	13460.02	16.08	29.46
9	dAspen(2) + dConifer(2) + dHW(2) + dPJ(2) + dShrub(2) + dGrass(2) + dRock(2) + VRM + dRoads + dSprings + E + S + West	13474.43	30.48	31.73
10	dAspen + dConifer + dHW + dPJ + dGrass + dRock + VRM(2) + dRoads(2) + dSprings(2) + West	13580.11	136.17	28.20
11	dAspen + dConifer + dHW + dPJ + dGrass + dRock + VRM + dRoads + dSprings + East + South + West	13603.84	159.90	23.49
12	dAspen + dConifer + dHW + dPJ + dShrub + dGrass + dRock + VRM + dRoads + East + South + West	13604.00	160.06	23.53
13	dAspen + dConifer + dHW + dPJ + dShrub + dRock + VRM + dRoads + dSprings + East + South + West	13605.18	161.24	23.60
14	dAspen + dConifer + dHW + dPJ + dShrub + dGrass + dRock + VRM + dRoads + dSprings + West	13605.93	161.98	24.48
15	dAspen + dConifer + dHW + dPJ + dShrub + dGrass + VRM + dRoads + dSprings + East + South + West	13608.41	164.47	23.85
16	Null Model	14190.70	746.76	11.50

Table B4. Model selection output for the cougar kill site selection model. Models are ranked by the estimated leave-one-out information criterion. PJ stands for pinyon and juniper cover, HW for hardwood cover, and VRM for the vector ruggedness metric. Coefficients with preceding 'd' indicate a distance-based metric and those followed by (2) indicate a second order polynomial.

Model	Coefficients	LOOic	ΔLOOic	K
1	dTreeCover(2) + Elev(2) + VRM(2) + Slope(2) + dRoads(2) + dSprings(2) + E + S + W + NoAsp	14774.62	0.00	21.25
2	dTreeCover(2) + Elev(2) + VRM(2) + Slope(2) + dRoads(2) + dSprings + E + S + W + NoAsp	14801.36	26.74	19.22
3	dTreeCover + Elev(2) + VRM(2) + Slope(2) + dRoads(2) + dSprings + E + S + W + NoAsp	14807.19	32.57	19.02
4	dTreeCover(2) + Elev(2) + VRM(2) + Slope(2) + dRoads + dSprings(2) + E + S + W + NoAsp	14848.22	73.60	21.12
5	dTreeCover(2) + Elev(2) + VRM(2) + Slope(2) + dRoads + dSprings(2) + E + S + W + NoAsp	14848.22	73.60	21.12
6	dTreeCover(2) + Elev(2) + VRM(2) + Slope(2) + dRoads + dSprings + E + S + W + NoAsp	14878.69	104.07	18.82
7	dTreeCover + Elev + VRM + Slope + dRoads + dSprings + E + S + W + NoAsp	15594.54	819.93	13.47
8	dTreeCover + Elev + VRM + dRoads + dSprings + E + S + W + NoAsp	15624.41	849.79	12.72
9	Null Model	17451.99	2677.37	4.76

Table B5. The detection parameter for a distance-based hazard function (sigma) and beta estimates for a hierarchical distance model for lagomorph abundance. Lower and upper CI are corresponding 95% posterior credible interval limits.

Distance Hazard Function	**mean**	**SD**	**Lower CI**	**Upper CI**
sigma	2.970	0.042	2.889	3.054
Lambda	**mean**	**SD**	**Lower CI**	**Upper CI**
Intercept	0.634	0.095	0.445	0.821
Year	0.466	0.027	0.415	0.521
Elevation	-0.749	0.060	-0.868	-0.630
Elevation^2	-0.568	0.049	-0.665	-0.473
% Forest Cover	-0.961	0.048	-1.060	-0.871
% Forest Cover^2	0.281	0.067	0.144	0.400

Table B6. The detection (p) and beta estimates (lambda) for a community N-mixture model for small mammal populations. Lower and upper CI are corresponding 95% posterior credible interval limits.

	Detection	**mean**	**SD**	**Lower CI**	**Upper CI**
	p (Mice)	0.584	0.035	0.509	0.646
	p (Chipmunks)	0.391	0.287	0.478	0.486
	p (Woodrats)	0.416	0.096	0.222	0.593
	p (Voles)	0.284	0.097	0.107	0.483
	p (Squirrels)	0.181	0.107	0.022	0.414
	Lambda	**mean**	**SD**	**Lower CI**	**Upper CI**
Mice	*Intercept*	2.016	0.132	1.761	2.273
	2013	0.489	0.139	0.211	0.766
	2014	-0.473	0.158	-0.777	-0.166
	2015	-0.350	0.152	-0.651	-0.052
	Elevation	0.138	0.056	0.031	0.248
	Elevation^2	-0.136	0.062	-0.263	-0.015
Chipmunks	*Intercept*	0.950	0.512	1.388	1.278
	2013	0.649	0.218	0.220	1.077
	2014	0.554	0.219	0.135	0.981
	2015	-0.060	0.244	-0.530	0.417
	Elevation	-0.170	0.106	-0.385	0.031
	Elevation^2	-0.360	0.111	-0.586	-0.143
	% Forest Cover	0.309	0.099	0.119	0.509
Woodrats	*Intercept*	-1.565	0.570	-2.717	-0.504
	2013	0.001	0.681	-1.358	1.317
	2014	-0.404	0.734	-1.898	1.002
	2015	-0.067	0.672	-1.412	1.238
	Elevation	1.462	0.576	0.482	2.746
	Elevation^2	-1.197	0.514	-2.320	-0.329
Voles	*Intercept*	-1.181	0.576	-2.298	0.021
	2013	0.013	0.533	-1.044	1.049
	2014	-1.293	0.766	-2.917	0.092
	2015	-2.824	1.200	-5.426	-0.791
	Elevation	-0.150	0.246	-0.638	0.334
	Elevation^2	0.126	0.268	-0.438	0.610
Squirrels	*Intercept*	-1.704	0.952	-3.472	0.327
	2013	1.830	0.729	0.471	3.340
	2014	0.114	0.923	-1.777	1.869
	2015	0.106	0.921	-1.762	1.879
	Elevation	0.716	0.403	0.003	1.600
	Elevation^2	-0.713	0.401	-1.577	-0.023

Table B7. Model selection output for the parturient deer summer site selection (2nd order). Models are ranked by the estimated leave-one-out information criterion. PJ stands for pinyon and juniper cover, HW for hardwood cover, and VRM for the vector ruggedness metric. Coefficients with preceding 'd' indicate a distance-based metric and those followed by (2) indicate a second order polynomial.

Model	Coefficients	LOOic	ΔLOOic	K
1	dRoads(2) + NDVI(2) + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	70003.49	0.00	23.93
2	dRoads + NDVI(2) + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	70103.75	100.26	23.48
3	dRoads + NDVI(2) + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	70589.71	586.22	21.64
4	dRoads + NDVI(2) + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	71892.77	1889.28	17.23
5	dRoads + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings(2) + E + S + W + NoAsp	73838.49	3835.00	20.77
6	dRoads(2) + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW()2 + dSprings + E + S + W + NoAsp	74669.76	4666.28	21.15
7	dRoads + NDVI + VRM(2) + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	74787.01	4783.52	21.55
8	dRoads + NDVI + VRM + dShrubs(2) + dGrass(2) + dAspen(2) + dPJ(2) + dConifer + dHW(2) + dSprings + E + S + W + NoAsp	74790.79	4787.30	20.27
9	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings(2) + E + S + W + NoAsp	74935.23	4931.74	17.73
10	DRoads(2) + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75772.99	5769.50	17.71
11	dRoads + NDVI + VRM(2) + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75859.48	5855.99	17.16
12	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings + E + S + W + NoAsp	75863.39	5859.90	16.40
13	dRoads + NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	76969.25	6965.76	15.94
14	dRoads + NDVI + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	76993.37	6989.88	15.21
15	NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77050.25	7046.76	15.03
16	NDVI + VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77050.25	7046.76	15.03
17	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + E + S + W + NoAsp	77147.97	7144.49	12.58

Table B7. cont.

18	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW + dSprings	77323.36	7319.88	9.36
19	NDVI + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78017.03	8013.54	9.81
20	dRoads + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78035.02	8031.54	9.92
21	VRM + dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78058.18	8054.69	9.91
22	dShrubs + dGrass + dAspen + dPJ + dConifer + dHW	78094.50	8091.01	9.26
23	Null Fixed	89287.99	19284.51	3.54

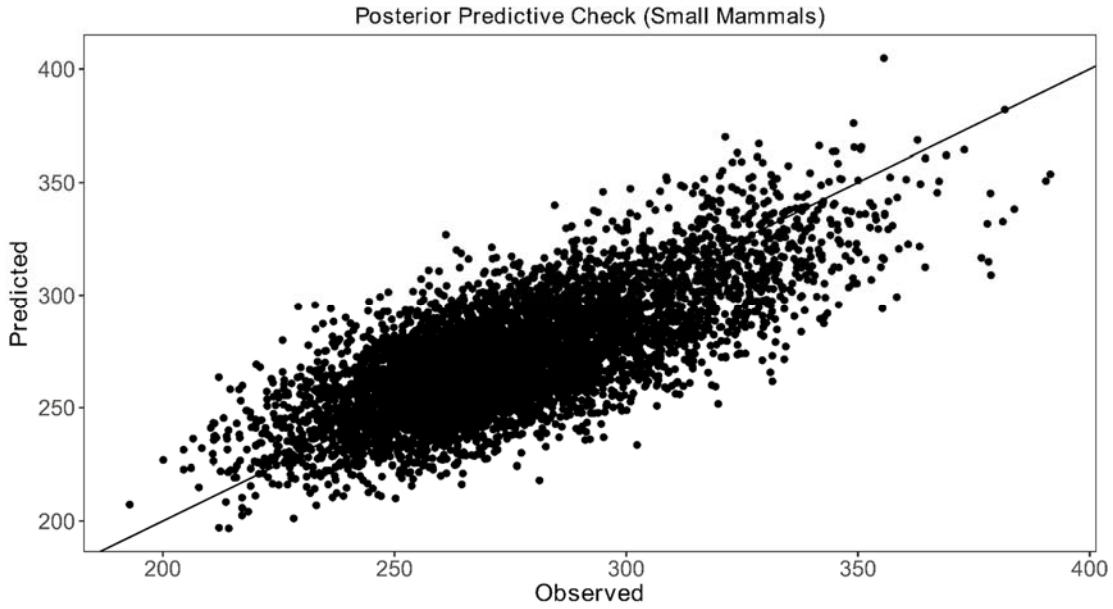

Figure B1. Posterior predictive checks for a community N-mixture model with negative binomial errors used to estimate small mammal abundance.

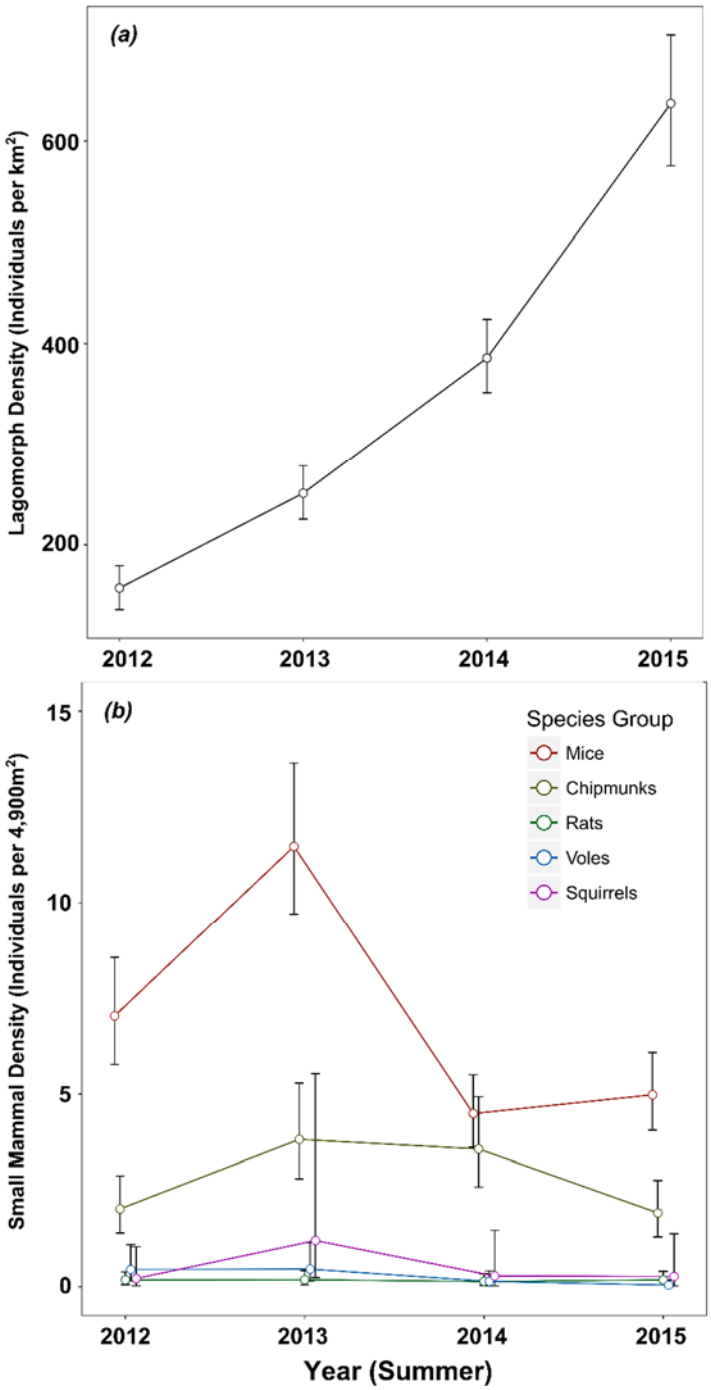

Figure B2. Estimated annual trends in lagomorphs (a) and small mammals (b) over the four years of the study.

APPENDIX C. CHAPTER 4 SUPPLEMENTARY TABLES

TABLE C1. Total counts of cougar kills by species and year. Values in parentheses indicate percentage of overall diet. The other category contains coyotes (*Canis latrans*), beaver (*Castor canadensis*), golden eagle (*Aquila chrysaetos*), domestic sheep, and cattle.

Year	Elk	Deer	Other	Annual Total
2011	2	5	0	7
2012	21	55	7	83
2013	28	69	6	103
2014	19	58	7	84
2015	4	1	0	5
Species Total	74 (26.2)	188 (66.7)	20 (7.1)	282

TABLE C2. Elk model selection table showing all top models (ΔQIC < 4) by month. K is the number of parameters in a given model. Covariates starting with a 'd' represent distance metrics, while those ending in (2) indicate a second order polynomial.

Month	Model	K	QIC	ΔQIC
February	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation + NDVI(2) + S + E	10	48039.41	0.00
February	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation + VRM + NDVI(2) + S + E	11	48041.69	2.29
February	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation + VRM(2) + NDVI(2) + S + E	12	48042.31	2.90
February	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation + NDVI(2) + S + E	9	48042.61	3.20
March	Elevation + dPJ(2) + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E + VRM	11	53978.63	0.00
March	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E + VRM	10	53979.33	0.70
March	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E + VRM	12	53980.43	1.80
March	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E + VRM	11	53981.15	2.52
March	Elevation + dPJ(2) + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	12	53981.78	3.15
March	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	11	53982.48	3.85
April	dAspen + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ + NDVI(2) + S + E	11	52226.29	0.00
April	dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ + NDVI(2) + S + E	12	52226.43	0.13
April	dAspen(2) + dConifer + dGrass(2) + dHardwood(2) + dPJ + NDVI(2) + S + E	11	52226.69	0.40
April	dAspen + dConifer + dPJ + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	10	52227.09	0.80

TABLE C2. cont.

April	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI(2) + S + E	14	52228.16	1.87
April	dAspen + dPJ + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI(2) + S + E	13	52228.28	1.99
April	dAspen + dConifer + dGrass + dHardwood + dPJ + dSprings + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52228.52	2.23
April	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	13	52228.78	2.49
April	dAspen + dPJ + dTertiaryRoads + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52228.85	2.56
April	dPJ + dTertiaryRoads + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	13	52228.91	2.62
April	dConifer + dPJ + dAspen(2) + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI(2) + S + E	13	52228.95	2.66
April	dConifer + dPJ + dSprings + dAspen(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52229.28	2.99
April	dConifer + dPJ + dTertiaryRoads + dAspen(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52229.37	3.08
April	dAspen + dConifer + dPJ + dSprings + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	11	52229.56	3.27
April	dAspen + dConifer + dPJ + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI(2) + S + E	12	52229.63	3.34
April	dAspen + dPJ + dConifer(2) + dGrass(2) + dHardwood(2) + dTertiaryRoads(2) + NDVI(2) + S + E	13	52229.69	3.40
April	dAspen + dPJ + dShrub + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52229.71	3.42

TABLE C2. cont.

April	dAspen + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + NDVI(2) + S + E	12	52229.82	3.53
April	dAspen + dConifer + dPJ + dTertiaryRoads + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	11	52229.86	3.56
April	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dTertiaryRoads(2) + NDVI(2) + S + E	14	52229.89	3.60
April	dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	13	52229.99	3.70
April	dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + NDVI(2) + S + E	13	52230.20	3.91
April	dConifer + dPJ + dAspen(2) + dGrass(2) + dHardwood(2) + dTertiaryRoads(2) + NDVI(2) + S + E	13	52230.21	3.91
April	dConifer + dPJ + dShrub + dAspen(2) + dGrass(2) + dHardwood(2) + NDVI(2) + S + E	12	52230.27	3.98
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + NDVI + S + E	9	51618.28	0.00
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + dSprings(2) + NDVI + S + E	11	51619.75	1.47
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + S + E	8	51620.24	1.96
May	dConifer + dHardwood + dAspen(2) + dGrass(2) + dPJ(2) + NDVI + S + E	10	51620.29	2.01
May	dAspen + dConifer + dHardwood + dShrub + dGrass(2) + dPJ(2) + NDVI + S + E	10	51620.75	2.47
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + NDVI + S + E + VRM	10	51620.86	2.58
May	dAspen + dHardwood + dConifer(2) + dGrass(2) + dPJ(2) + NDVI + S + E	10	51621.18	2.90
May	dAspen + dConifer + dGrass(2) + dHardwood(2) + dPJ(2) + NDVI + S + E	10	51621.35	3.07

TABLE C2. cont.

May	dAspen + dConifer + dHardwood + dTertiaryRoads + dGrass(2) + dPJ(2) + NDVI + S + E	10	51621.67	3.39
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + NDVI(2) + S + E	10	51621.85	3.58
May	dAspen + dConifer + dHardwood + dGrass(2) + dPJ(2) + dSprings(2) + S + E	10	51621.91	3.64
May	dAspen + dConifer + dHardwood + dSprings + dGrass(2) + dPJ(2) + NDVI + S + E	10	51621.93	3.65
May	dConifer + dHardwood + dAspen(2) + dGrass(2) + dPJ(2) + S + E	9	51622.07	3.79
June	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dShrub(2) + NDVI(2) + S + E + VRM	16	47407.38	0.00
June	dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + dShrub(2) + NDVI(2) + S + E + VRM	17	47407.95	0.57
June	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dShrub(2) + NDVI(2) + VRM(2) + S + E	17	47409.78	2.40
June	dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + dShrub(2) + NDVI(2) + VRM(2) + S + E	18	47410.33	2.95
July	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI + S + E + VRM	14	47695.02	0.00
July	dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + dSprings(2) + NDVI + S + E + VRM	15	47696.47	1.45
July	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + VRM(2) + NDVI + S + E	15	47696.66	1.64
July	dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dPJ(2) + dSprings(2) + VRM(2) + NDVI + S + E	16	47698.14	3.12
July	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + NDVI(2) + S + E + VRM	15	47698.80	3.78

TABLE C2. cont.

July	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	16	47698.87	3.85
July	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dShrub(2) + dSprings(2) + NDVI + S + E + VRM	16	47698.92	3.90
August	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	16	47731.85	0.00
August	dHardwood + dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	16	47731.87	0.02
August	dHardwood + dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47732.01	0.16
August	dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	15	47732.20	0.34
August	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dSprings(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47733.44	1.59
August	dHardwood + dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dSprings(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	18	47733.64	1.79
August	dHardwood + dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dSprings(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47733.64	1.79
August	dHardwood + dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + NDVI + S + E	15	47733.70	1.85
August	dHardwood + dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + NDVI + S + E	16	47733.85	2.00
August	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	15	47733.88	2.03

TABLE C2. cont.

August	dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dSprings(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	16	47733.94	2.09
August	dGrass + dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	14	47734.22	2.37
August	dHardwood + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dPJ(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47734.61	2.76
August	dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dPJ(2) + dShrub(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47734.68	2.83
August	dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dPJ(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	16	47734.75	2.89
August	dHardwood + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dPJ(2) + dShrub(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	18	47734.96	3.11
August	dHardwood + dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + NDVI + S + E	14	47735.02	3.17
August	dHardwood + dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	15	47735.15	3.30
August	dHardwood + dPJ + dSprings + dTertiaryRoads + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + NDVI + S + E	15	47735.17	3.31
August	dHardwood + dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	15	47735.33	3.48
August	dHardwood + dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	16	47735.44	3.59
August	dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	16	47735.45	3.60

TABLE C2. cont.

August	dHardwood + dPJ + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	17	47735.45	3.60
August	dPJ + dShrub + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	17	47735.49	3.64
August	dPJ + dShrub + dAspen(2) + dConifer(2) + dGrass(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	14	47735.50	3.65
August	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dHardwood(2) + dShrub(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	18	47735.57	3.71
August	dPJ + dSprings + dAspen(2) + dConifer(2) + dGrass(2) + dShrub(2) + dTertiaryRoads(2) + NDVI + S + E	14	47735.64	3.79
September	dPJ + Elevation + dTertiaryRoads(2) + NDVI(2) + S + E	7	48057.53	0.00
September	Elevation + dTertiaryRoads(2) + NDVI(2) + S + E	6	48057.56	0.04
September	dPJ + Elevation + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	9	48058.04	0.51
September	Elevation + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	8	48058.58	1.05
September	dPJ + Elevation + dTertiaryRoads(2) + NDVI(2) + S + E + VRM	8	48058.71	1.19
September	dPJ + dShrub + Elevation + dTertiaryRoads(2) + NDVI(2) + S + E	8	48058.93	1.41
September	Elevation + dTertiaryRoads(2) + NDVI(2) + S + E + VRM	7	48058.98	1.46
September	dPJ + dShrub + Elevation + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	10	48059.38	1.85
September	dPJ + dShrub + Elevation + dTertiaryRoads(2) + NDVI(2) + S + E	9	48060.07	2.54
September	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E	9	48060.14	2.61

TABLE C2. cont.

September	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E	8	48060.30	2.77
October	dPJ + dTertiaryRoads + dShrub(2) + Elevation(2) + NDVI(2) + S + E + VRM	10	50022.02	0.00
October	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E + VRM	11	50023.10	1.08
October	dPJ + dTertiaryRoads + dShrub(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	11	50023.14	1.12
October	dPJ + dTertiaryRoads + Elevation + dShrub(2) + NDVI(2) + S + E + VRM	9	50023.39	1.36
October	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	12	50024.20	2.18
October	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E + VRM	10	50024.55	2.52
October	dPJ + dTertiaryRoads + Elevation + dShrub(2) + NDVI(2) + VRM(2) + S + E	10	50024.63	2.61
October	dTertiaryRoads + dPJ(2) + dShrub(2) + Elevation(2) + NDVI(2) + S + E + VRM	11	50025.00	2.97
October	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	11	50025.77	3.75
November	dPJ + dTertiaryRoads + dShrub(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	11	47549.17	0.00
November	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	12	47551.38	2.21
November	dTertiaryRoads + dPJ(2) + dShrub(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	12	47551.41	2.24
November	dPJ + dTertiaryRoads + Elevation + dShrub(2) + NDVI(2) + VRM(2) + S + E	10	47552.79	3.61
December	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	12	46965.68	0.00
December	dPJ + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E	11	46965.72	0.04

TABLE C2. cont.

December	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + VRM(2) + S + E	11	46967.52	1.84
December	dPJ + Elevation + dShrub(2) + dTertiaryRoads(2) + NDVI(2) + S + E	10	46967.94	2.26
December	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	13	46968.70	3.02
December	dPJ(2) + dShrub(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E + VRM	12	46968.74	3.06
December	dPJ + dShrub(2) + Elevation(2) + NDVI(2) + S + E + VRM	9	46969.21	3.53
December	dPJ + dShrub(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	10	46969.37	3.69

TABLE C3. Deer model selection table showing all top models (ΔQIC < 4) by month. K is the number of parameters in a given model. Covariates starting with a 'd' represent distance metrics, while those ending in (2) indicate a second order polynomial. VRM is the vector ruggedness metric.

Month	Model	K	QIC	ΔQIC
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dSprings(2) + NDVI + S + E + VRM	12	24720.98	0.00
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	13	24721.84	0.86
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dPJ(2) + dSprings(2) + NDVI + S + E + VRM	13	24723.23	2.25
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dSprings(2) + VRM(2) + NDVI + S + E + VRM	13	24723.60	2.61
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dShrubs(2) + dSprings(2) + NDVI + S + E + VRM	13	24723.70	2.72
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dSprings(2) + S + E + VRM	11	24723.82	2.83
January	dConifer + dHardwood + dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + dPJ(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	14	24724.10	3.11
January	dPJ + dShrubs + dConifer(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	14	24724.31	3.33
January	dShrubs + dTertiaryRoads + dConifer(2) + dHardwood(2) + dSprings(2) + NDVI + S + E + VRM	11	24724.46	3.47

TABLE C3. cont.

January	dPJ + dConifer(2) + dHardwood(2) + dShrubs(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E + VRM	14	24724.47	3.49
January	dPJ + dShrubs + dSprings + dTertiaryRoads + dConifer(2) + dHardwood(2) + NDVI + S + E + VRM	11	24724.96	3.97
February	dAspen + dHardwood + dShrubs + dSprings + dConifer(2) + S + E + VRM	8	22497.08	0.00
February	dAspen + dHardwood + dShrubs + dConifer(2) + S + E + VRM	7	22497.23	0.15
February	dAspen + dHardwood + dShrubs + dSprings + dConifer(2) + VRM(2) + S + E	9	22497.72	0.64
February	dAspen + dHardwood + dShrubs + dConifer(2) + VRM(2) + S + E	8	22497.86	0.78
February	dHardwood + dShrubs + dAspen(2) + dConifer(2) + S + E + VRM	8	22498.44	1.36
February	dAspen + dHardwood + dShrubs + dSprings + dConifer(2) + dPJ(2) + S + E + VRM	10	22498.49	1.40
February	dHardwood + dShrubs + dAspen(2) + dConifer(2) + VRM(2) + S + E	9	22499.11	2.03
February	dAspen + dHardwood + dShrubs + dSprings + dConifer(2) + dPJ(2) + VRM(2) + S + E	11	22499.23	2.15
February	dAspen + dHardwood + dShrubs + dConifer(2) + dPJ(2) + S + E + VRM	9	22499.24	2.16
February	dAspen + dHardwood + dShrubs + dConifer(2) + dPJ(2) + VRM(2) + S + E	10	22499.98	2.90
February	dHardwood + dShrubs + dSprings + dAspen(2) + dConifer(2) + S + E + VRM	9	22500.14	3.06
February	dHardwood + dShrubs + dAspen(2) + dConifer(2) + dPJ(2) + S + E + VRM	10	22500.18	3.09
February	dAspen + dHardwood + dShrubs + dSprings + dConifer(2) + NDVI + S + E + VRM	9	22500.73	3.65
February	dAspen + dHardwood + dPJ + dShrubs + dSprings + dConifer(2) + S + E + VRM	9	22500.78	3.70
February	dHardwood + dShrubs + dSprings + dAspen(2) + dConifer(2) + VRM(2) + S + E	10	22500.81	3.72

TABLE C3. cont.

February	dAspen + dHardwood + dPJ + dShrubs + dConifer(2) + S + E + VRM	8	22500.81	3.72
February	dHardwood + dShrubs + dAspen(2) + dConifer(2) + dPJ(2) + VRM(2) + S + E	11	22500.95	3.87
March	dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E	11	35986.47	0.00
March	dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E + VRM	12	35988.21	1.74
March	dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + VRM(2) + S + E	13	35989.42	2.94
March	dShrubs + dPJ(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E	10	35989.54	3.07
March	dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + Elevation(2) + NDVI(2) + S + E	10	35990.03	3.56
April	dConifer + dPJ + dAspen(2) + dGrass(2) + dShrubs(2) + dTertiaryRoads(2) + VRM(2) + S + E	13	37057.01	0.00
April	dConifer + dAspen(2) + dGrass(2) + dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + VRM(2) + S + E	14	37058.37	1.36
April	dConifer + dPJ dAspen(2) + dGrass(2) + dShrubs(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E + VRM	14	37059.66	2.65
April	dConifer + dAspen(2) + dGrass(2) + dPJ(2) + dShrubs(2) + dTertiaryRoads(2) + VRM(2) + NDVI + S + E	15	37060.99	3.97
May	dConifer + dSprings + dTertiaryRoads + dAspen(2) + dShrubs(2) + VRM(2) + S + E	10	34793.24	0.00
May	dSprings + dTertiaryRoads + dAspen(2) + dConifer(2) + dShrubs(2) + VRM(2) + S + E	11	34794.40	1.17
May	dTertiaryRoads + dAspen(2) + dConifer(2) + dShrubs(2) + VRM(2) + S + E	10	34794.63	1.40
May	dConifer + dTertiaryRoads + dAspen(2) + dShrubs(2) + VRM(2) + S + E	9	34794.83	1.59

TABLE C3. cont.

May	dConifer + dSprings + dTertiaryRoads + dAspen(2) + dShrubs(2) + VRM(2) + NDVI + S + E	11	34795.01	1.77
May	dConifer + dShrubs + dSprings + dTertiaryRoads + dAspen(2) + VRM(2) + S + E	9	34795.63	2.40
May	dSprings + dAspen(2) + dConifer(2) + dShrubs(2) + VRM(2) + S + E	10	34795.79	2.55
May	dSprings + dTertiaryRoads + dAspen(2) + dConifer(2) + dShrubs(2) + VRM(2) + NDVI + S + E	12	34795.87	2.63
June	dShrubs + dTertiaryRoads + dAspen(2) + VRM(2) + S + E	7	31463.66	0.00
June	dShrubs + dTertiaryRoads + dAspen(2) + S + E	5	31464.86	1.20
June	dShrubs + dSprings + dTertiaryRoads + dAspen(2) + VRM(2) + S + E	8	31467.99	4.33
July	dShrubs + dTertiaryRoads + dAspen(2) + NDVI + S + E	6	31555.27	0.00
July	dShrubs + dSprings + dTertiaryRoads + dAspen(2) + NDVI + S + E	7	31556.11	0.83
July	dTertiaryRoads + dAspen(2) + dShrubs(2) + NDVI + S + E	7	31557.64	2.37
July	dShrubs + dTertiaryRoads + dAspen(2) + NDVI + S + E + VRM	7	31557.97	2.69
July	dSprings + dTertiaryRoads + dAspen(2) + dShrubs(2) + NDVI + S + E	8	31558.10	2.83
July	dShrubs + dSprings + dTertiaryRoads + dAspen(2) + NDVI + S + E + VRM	8	31558.83	3.56
August	dShrubs + dAspen(2) + NDVI(2) + S + E	6	31358.41	0.00
August	dShrubs + dTertiaryRoads + dAspen(2) + NDVI(2) + S + E	7	31359.02	0.60
August	dShrubs + dTertiaryRoads + dAspen(2) + dSprings(2) + NDVI(2) + S + E	9	31360.06	1.65
August	dShrubs + dAspen(2) + dSprings(2) + NDVI(2) + S + E	8	31360.29	1.88
August	dShrubs + dAspen(2) + dTertiaryRoads(2) + NDVI(2) + S + E	8	31361.74	3.33
August	dShrubs + dSprings + dAspen(2) + NDVI(2) + S + E	7	31362.28	3.86
September	dAspen(2) + dSprings(2) + dTertiaryRoads(2) + NDVI(2) + S + E	9	29653.15	0.00

TABLE C3. cont.

September	dGrass + dAspen(2) + dSprings(2) + dTertiaryRoads(2) + NDVI(2) + S + E	10	29655.95	2.80
October	dAspen(2) + dHardwood(2) + dTertiaryRoads(2) + NDVI + S + E	8	27011.36	0.00
October	dAspen(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + NDVI + S + E	10	27011.71	0.35
October	dAspen(2) + dHardwood(2) + NDVI + S + E	6	27012.27	0.92
October	dSprings + dAspen(2) + dHardwood(2) + dTertiaryRoads(2) + NDVI + S + E	9	27014.85	3.49
November	dPJ + dTertiaryRoads(2) + Elevation(2) + S + E	6	24719.29	0.00
November	dPJ + dTertiaryRoads(2) + Elevation(2) + VRM(2) + S + E	8	24719.80	0.51
November	dPJ(2) + dTertiaryRoads(2) + Elevation(2) + S + E	7	24721.41	2.12
November	dPJ + dTertiaryRoads(2) + Elevation(2) + S + E + VRM	7	24721.61	2.31
November	dPJ(2) + dTertiaryRoads(2) + Elevation(2) + VRM(2) + S + E	9	24722.77	3.48
November	dPJ + dTertiaryRoads(2) + Elevation(2) + NDVI + S + E	7	24722.79	3.50
November	dPJ + dTertiaryRoads(2) + Elevation(2) + VRM(2) + NDVI + S + E	9	24723.24	3.95
December	dShrubs + dSprings + dConifer(2) + S + E	5	25678.61	0.00
December	dShrubs + dConifer(2) + dSprings(2) + dTertiaryRoads(2) + S + E	8	25678.89	0.28
December	dShrubs + dConifer(2) + dSprings(2) + S + E	6	25679.12	0.51
December	dShrubs + dAspen(2) + dConifer(2) + dSprings(2) + S + E	8	25679.32	0.71
December	dShrubs + dSprings + dAspen(2) + dConifer(2) + S + E	7	25679.38	0.78
December	dShrubs + dSprings + dConifer(2) + S + E + VRM	6	25680.33	1.72
December	dShrubs + dSprings + dAspen(2) + dConifer(2) + S + E + VRM	8	25680.90	2.29
December	dShrubs + dAspen(2) + dConifer(2) + dHardwood(2) + dSprings(2) + S + E	10	25681.05	2.44
December	dShrubs + dConifer(2) + dSprings(2) + S + E + VRM	7	25681.09	2.48
December	dShrubs + dAspen(2) + dConifer(2) + dSprings(2) + S + E + VRM	9	25681.11	2.50
December	dShrubs + dConifer(2) + dSprings(2) + dTertiaryRoads(2) + S + E + VRM	9	25681.16	2.55

TABLE C3. cont.

December	dShrubs + dAspen(2) + dConifer(2) + dSprings(2) + dTertiaryRoads(2) + S + E	10	25681.20	2.59
December	dShrubs + dConifer(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + S + E	10	25681.40	2.79
December	dAspen + dShrubs + dConifer(2) + dSprings(2) + dTertiaryRoads(2) + S + E	9	25681.68	3.07
December	dShrubs + dSprings + dConifer(2) + dHardwood(2) + S + E	7	25681.75	3.14
December	dAspen + dShrubs + dSprings + dConifer(2) + S + E	6	25681.79	3.19
December	dShrubs + dConifer(2) + dHardwood(2) + dSprings(2) + S + E	8	25681.88	3.28
December	dAspen + dShrubs + dConifer(2) + dSprings(2) + S + E	7	25681.96	3.35
December	dShrubs + dSprings + dAspen(2) + dConifer(2) + dHardwood(2) + S + E	9	25682.08	3.48
December	dShrubs + dSprings + dConifer(2) + dTertiaryRoads(2) + S + E	7	25682.39	3.78
December	dShrubs + dAspen(2) + dConifer(2) + dHardwood(2) + dSprings(2) + dTertiaryRoads(2) + S + E	12	25682.40	3.79
December	dShrubs + dAspen(2) + dConifer(2) + dHardwood(2) + dSprings(2) + S + E + VRM	11	25682.52	3.91

TABLE C4. Coefficient estimates from the elk step-selection function by monthly interval. Values in parentheses represent the 95% confidence intervals and dashes values that were not estimated. A leading 'd' in coefficient names represents 'distance to'. PJ represents pinyon and juniper cover and VRM the vector ruggedness metric. The reference group for aspect is North, West, and no aspect.

Coefficient Name	January	February	March	April	May	June
dAspen	-	-	-	-0.18 (-0.26, -0.09)	-0.14 (-0.28, -0.00)	-0.33 (-0.64, -0.03)
dAspen^2	-	-	-	-	-	0.08 (-0.00, 0.18)
dConifer	-	-	-	0.25 (0.16, 0.34)	0.25 (0.16, 0.35)	0.51 (0.32, 0.70)
dConifer^2	-	-	-	-0.02 (-0.04, 0.00)	-	-0.24 (-0.36, -0.12)
dHardwood	-	-	-	0.11 (0.03, 0.19)	-0.09 (-0.16, -0.03)	-0.15 (-0.27, -0.03)
dHardwood^2	-	-	-	-0.02 (-0.05, -0.00)	-	0.05 (0.00, 0.10)
dPJ	-0.63 (-0.90, -0.36)	-0.84 (-1.15, -0.53)	-0.35 (-0.65, -0.04)	-0.54 (-0.72, -0.36)	-0.25 (-0.41, -0.08)	0.20 (0.10, 0.31)
dPJ^2	-	-0.32 (-0.67, 0.03)	-	-	0.07 (0.02, 0.12)	-
dPJ:Daylight	-	-	-0.40 -0.62, -0.18)	-	-	-0.03 (-0.08, 0.01)
dShrub	0.10 (0.02, 0.18)	0.27 (0.12, 0.41)	0.20 (0.04, 0.36)	-	-	0.26 (0.00, 0.52)
dShrub^2	-	-0.06 (-0.13, -0.00)	-0.07 (-0.13, -0.01)	-	-	-0.30 (-0.46, -0.14)
dShrub:Daylight	-	-	-	-	-	-
dGrass	-	-	-	-0.24 (-0.35, -0.13)	-0.40 (-0.52, -0.28)	-0.35 (-0.54, -0.16)
dGrass^2	-	-	-	0.03 (0.00, 0.06)	0.05 (0.01, 0.09)	0.08 (0.04, 0.12)
dGrass:Daylight	-	-	-	0.12 (0.08, 0.16)	0.21 (0.12, 0.31)	-
dGrass^2:Daylight	-	-	-	-	-0.04 (-0.08, -0.01)	-
dSprings	-	-	-	-	-	-0.40 (-0.53, -0.26)

TABLE C4. cont.

dSprings^2	-	-	-	-	-	-
dTertiaryRoads	-	-0.12 (-0.21, -0.02)	-0.10 (-0.20, -0.00)	-	-	-
dTertiaryRoads^2	-	-0.05 (-0.10, -0.00)	-0.06 (-0.14, 0.00)	-	-	-
NDVI	-0.12 (-0.26, 0.00)	-0.67 (-0.96, -0.37)	-0.49 (-0.66, -0.32)	-0.20 (-0.34, -0.05)	0.10 (-0.02, 0.22)	0.63 (0.36, 0.90)
NDVI^2	-	-0.49 (-0.72, -0.26)	-0.47 (-0.62, -0.31)	-0.22 (-0.39, -0.05)	-	-0.25 (-0.40, -0.10)
VRM	-	-	-0.04 (-0.07, -0.01)	-	-	0.03 (0.00, 0.05)
VRM^2	-	-	-	-	-	-
VRM:Daylight	-	-	-	-	-	-
VRM^2:Daylight	-	-	-	-	-	-
Elevation	1.11 (0.83, 1.39)	0.95 (0.67, 1.23)	0.76 (0.49, 1.02)	-	-	-
Elevation^2	0.12 (-0.03, 0.28)	-	-	-	-	-
Elevation:Daylight	-0.19 (-0.31, -0.07)	-0.17 (-0.30, -0.04)	-	-	-	-
Elevation^2:Daylight	-	-	-	-	-	-
South	0.42 (0.30, 0.53)	0.49 (0.36, 0.62)	0.27 (0.12, 0.41)	0.29 (0.20, 0.39)	0.00 (-0.12, 0.13)	-0.42 (-0.57, -0.28)
East	0.19 (0.09, 0.30)	0.31 (0.21, 0.40)	0.04 (-0.04, 0.13)	0.14 (0.05, 0.23)	0.13 (0.05, 0.22)	-0.07 (-0.16, 0.00)

Coefficient Name	July	August	September	October	November	December
dAspen	-0.68 (-0.91, -0.44)	-0.55 (-0.81, -0.30)	-	-	-	-
dAspen^2	0.12 (0.05, 0.18)	0.14 (0.05, 0.23)	-	-	-	-
dConifer	0.71 (0.52, 0.91)	0.60 (0.46, 0.74)	-	-	-	-
dConifer^2	-0.22 (-0.32, -0.13)	-0.21 (-0.31, -0.11)	-	-	-	-
dHardwood	-0.10 (-0.19, -0.01)	-	-	-	-	-
dHardwood^2	0.08 (0.04, 0.11)	-	-	-	-	-

TABLE C4. cont.

dPJ	0.29 (0.20, 0.38)	0.28 (0.21, 0.34)	-0.09 (-0.21, 0.03)	-0.14 (-0.23, -0.05)	-0.65 (-0.77, -0.53)	-0.98 (-1.18, -0.78)
dPJ^2	-	-	-	-	-	-
dPJ:Daylight	-	-	-	-	-	-
dShrub	-	0.12 (-0.05, 0.31)	-	0.19 (0.03, 0.34)	0.15 (0.10, 0.19)	0.28 (0.12, 0.45)
dShrub^2	-	-0.04 (-0.10, 0.01)	-	-0.08 (-0.14, -0.02)	-	-0.07 (-0.12, -0.02)
dShrub:Daylight	-	0.11 (0.01, 0.21)	-	-	-	-
dGrass	-0.54 (-0.74, -0.34)	-0.41 (-0.58, -0.24)	-	-	-	-
dGrass^2	0.12 (0.08, 0.16)	0.10 (0.07, 0.13)	-	-	-	-
dGrass:Daylight	-	-	-	-	-	-
dGrass^2:Daylight	-	-	-	-	-	-
dSprings	-0.21 (-0.35, -0.07)	-0.11 (-0.22, -0.00)	-	-	-	-
dSprings^2	-0.12 (-0.21, -0.03)	-	-	-	-	-
dTertiaryRoads	-	0.23 (0.13, 0.34)	0.24 (0.14, 0.35)	0.14 (0.07, 0.21)	0.09 (0.03, 0.16)	0.11 (-0.00, 0.22)
dTertiaryRoads^2	-	-0.10 (-0.15, -0.05)	-0.12 (-0.16, -0.08)	-	-	-0.04 (-0.08, -0.01)
NDVI	0.21 (0.01, 0.41)	0.26 (0.10, 0.43)	0.42 (0.14, 0.70)	0.02 (-0.14, 0.20)	-0.19 (-0.26, -0.12)	-0.26 (-0.50, -0.01)
NDVI^2	-	-	-0.16 (-0.31, -0.01)	-0.20 (-0.34, -0.07)	-0.15 (-0.22, -0.07)	-0.26 (-0.49, -0.02)
VRM	-0.06 (-0.09, -0.03)	-0.01 (-0.03, 0.01)	-	-0.05 (-0.07, -0.02)	-0.04 (-0.08, -0.01)	-0.04 (-0.08, -0.00)
VRM^2	-	0.01 (0.00, 0.02)	-	-	0.02 (0.00, 0.04)	0.02 (0.00, 0.05)
VRM:Daylight	0.05 (0.01, 0.10)	-	-	-	0.07 (0.03, 0.12)	0.03 (-0.00, 0.07)
VRM^2:Daylight	-	-	-	-	-	-0.02 (-0.05, -0.00)
Elevation	-	-	1.07 (0.85, 1.28)	0.91 (0.68, 1.14)	0.94 (0.74, 1.14)	1.08 (0.87, 1.30)
Elevation^2	-	-	-	-0.05 (-0.17, 0.07)	0.07 (-0.03, 0.18)	0.08 (-0.03, 0.20)
Elevation:Daylight	-	-	-0.21 (-0.36, -0.07)	-0.13 (-0.27, 0.00)	-	-

TABLE C4. cont.

				-0.07		
Elevation^2:Daylight	-	-	-	(-0.14, 0.00)	-	-
	-0.28	-0.09	-0.13	0.01	0.23	0.46
South	(-0.40, -0.16)	(-0.19, 0.01)	(-0.26, -0.00)	(-0.07, 0.11)	(0.11, 0.34)	(0.37, 0.56)
	-0.17	-0.12	-0.09	0.01	0.25	0.23
East	(-0.24, -0.10)	(-0.20, -0.05)	(-0.17, -0.00)	(-0.05, 0.09)	(0.15, 0.35)	(0.13, 0.34)

TABLE C5. Coefficient estimates from the deer step-selection function by monthly interval. Values in parentheses represent the 95% confidence intervals and dashes values that were not estimated. A leading 'd' in coefficient names represents 'distance to'. PJ represents pinyon and juniper cover and VRM the vector ruggedness metric. The reference group for aspect is North, West, and no aspect.

Coefficient Name	January	February	March	April	May	June
dAspen	-	0.32 (0.09, 0.56)	-	-0.03 (-0.28, 0.21)	-0.30 (-0.66, 0.05)	-1.03 (-1.67, -0.38)
dAspen^2	-	-	-	0.18 (0.02, 0.33)	0.44 (0.20, 0.67)	0.67 (0.31, 1.03)
dAspen:Daylight	-	-	-	-	-	-
dConifer	0.05 (-0.22, 0.33)	0.11 (-0.09, 0.31)	-	-0.24 (-0.40, -0.08)	-0.25 (-0.40, -0.10)	-
dConifer^2	-0.12 (-0.19, -0.05)	-0.09 (-0.16, -0.03)	-	-	-	-
dConifer:Daylight	-	-	-	0.26 (0.07, 0.45)	0.20 (0.06, 0.34)	-
dHardwood	0.39 (0.16, 0.62)	0.13 (-0.00, 0.27)	-	-	-	-
dHardwood^2	-0.08 (-0.16, -0.01)	-	-	-	-	-
dPJ	-0.18 (-0.40, 0.04)	-	-0.40 (-0.55, -0.24)	-0.51 (-0.67, -0.35)	-	-
dPJ^2	-	-	0.16 (0.07, 0.26)	-	-	-
dShrub	-0.42 (-0.57, -0.26)	-0.42 (-0.64, -0.20)	-0.34 (-0.54, -0.15)	0.04 (-0.08, 0.17)	-0.02 (-0.14, 0.10)	0.10 (0.03, 0.18)
dShrub^2	-	-	0.07 (0.03, 0.10)	-0.08 (-0.12, -0.04)	-0.02 (-0.05, 0.00)	-
dShrub:Daylight	-	0.12 (-0.03, 0.28)	0.29 (0.13, 0.45)	-	-	-
dShurb^2:Daylight	-	-	-0.08 (-0.12, -0.03)	-	-	-
dGrass	-	-	-	0.38 (0.20, 0.56)	-	-
dGrass^2	-	-	-	-0.24 (-0.34, -0.14)	-	-
dSprings	0.41 (0.11, 0.71)	0.20 (-0.07, 0.48)	-	-	-0.15 (-0.32, 0.02)	-
dSprings^2	-0.19 (-0.40, 0.01)	-	-	-	-	-
dTertiaryRoads	0.29 (0.02, 0.56)	-	0.18 (0.02, 0.34)	0.13 (-0.06, 0.33)	0.14 (-0.04, 0.34)	0.23 (0.00, 0.47)
dTertiaryRoads^2	-	-	-0.11 (-0.22, -0.00)	-0.35 (-0.49, -0.21)	-	-

TABLE C5. cont.

dTertiaryRoads:Daylight	-	-	-	-	-	-
NDVI	-0.18 (-0.41, 0.04)	-	-0.55 (-1.16, 0.05)	-	-	-
NDVI^2	-	-	-0.34 (-0.67, -0.01)	-	-	-
VRM	0.05 (0.00, 0.10)	0.05 (0.01, 0.09)	-	0.00 (-0.03, 0.04)	0.01 (-0.02, 0.06)	0.01 (-0.03, 0.06)
VRM^2	-	-	-	-0.06 (-0.10, -0.01)	-0.04 (-0.09, -0.00)	-0.05 (-0.10, 0.00)
Elevation	-	-	-3.13 (-4.14, -2.12)	-	-	-
Elevation^2	-	-	-1.50 (-1.96, -1.04)	-	-	-
South	-0.07 (-0.27, 0.12)	-0.09 (-0.26, 0.08)	-0.26 (-0.40, -0.11)	0.01 (-0.10, 0.13)	-0.14 (-0.31, 0.01)	-0.07 (-0.27, 0.12)
East	0.12 (-0.07, 0.31)	-0.08 (-0.25, 0.09)	-0.14 (-0.26, -0.01)	-0.04 (-0.20, 0.10)	0.01 (-0.13, 0.16)	0.13 (0.00, 0.25)

Coefficient Name	July	August	September	October	November	December
dAspen	-0.94 (-1.64, -0.25)	-0.23 (-0.93, 0.45)	-0.80 (-1.39, -0.22)	-0.64 (-1.07, -0.22)	-	-
dAspen^2	0.87 (0.47, 1.27)	0.69 (0.31, 1.07)	0.66 (0.36, 0.96)	0.48 (0.28, 0.67)	-	-
dAspen:Daylight	-	-0.54 (-0.85, -0.22)	-	-	-	-
dConifer	-	-	-	-	-	0.18 (-0.08, 0.45)
dConifer^2	-	-	-	-	-	-0.14 (-0.25, -0.04)
dConifer:Daylight	-	-	-	-	-	-
dHardwood	-	-	-	0.09 (-0.12, 0.31)	-	-
dHardwood^2	-	-	-	-0.24 (-0.40, -0.08)	-	-
dPJ	-	-	-	-	-0.26 (-0.43, -0.09)	-
dPJ^2	-	-	-	-	-	-
dShrub	0.17 (0.10, 0.24)	0.10 (-0.00, 0.22)	-	-	-	-0.20 (-0.40, -0.00)
dShrub^2	-	-	-	-	-	-
dShrub:Daylight	-	-	-	-	-	-0.14 (-0.26, -0.01)
dShurb^2:Daylight	-	-	-	-	-	-
dGrass	-	-	-	-	-	-

TABLE C5. cont.

dGrass^2	-	-	-	-	-	-
dSprings	-	-	-0.01 (-0.25, 0.22)	-	-	0.26 (0.00, 0.52)
dSprings^2	-	-	-0.24 (-0.39, -0.09)	-	-	-
dTertiaryRoads	0.19 (-0.05, 0.44)	-	0.08 (-0.20, 0.38)	-0.07 (-0.38, 0.23)	0.06 (-0.16, 0.29)	-
dTertiaryRoads^2	-	-	0.08 (0.02, 0.13)	0.08 (0.02, 0.14)	0.10 (0.04, 0.15)	-
dTertiaryRoads:Daylight	-	-	-	0.19 (-0.03, 0.42)	-	-
NDVI	-0.23 (-0.43, -0.02)	-0.29 (-0.47, -0.11)	-0.19 (-0.38, -0.00)	0.20 (0.03, 0.36)	-	-
NDVI^2	-	0.10 (-0.02, 0.22)	0.13 (0.02, 0.23)	-	-	-
VRM	-	-	-	-	-	-
VRM^2	-	-	-	-	-	-
Elevation	-	-	-	-	-0.48 (-1.38, 0.42)	-
Elevation^2	-	-	-	-	0.78 (0.40, 1.16)	-
South	0.00 (-0.15, 0.17)	0.11 (-0.06, 0.29)	0.11 (-0.04, 0.27)	0.02 (-0.21, 0.25)	0.11 (-0.14, 0.36)	0.23 (0.03, 0.42)
East	-0.01 (-0.13, 0.11)	0.02 (-0.09, 0.14)	0.05 (-0.10, 0.21)	-0.03 (-0.22, 0.15)	0.08 (-0.14, 0.31)	0.10 (-0.12, 0.32)

TABLE C6. Cougar model selection table showing all models evaluated. K is the number of parameters in a given model. Covariates starting with a 'd' represent distance metrics, while those ending in (2) indicate a second order polynomial. ElkProb and DeerProb represent estimated elk and deer relative probability of use, respectively. VRM is the vector ruggedness metric.

Coefficients	K	QIC	ΔQIC
E + S + W + Slope(2) + VRM(2)*Active(2)*Harvest + dTreeCover(2)*Harvest + dTertiaryRoads(2) + ElkProb*Harvest + DeerProb*Harvest	20	82241.39	0.00
E + S + W + Slope(2) + VRM(2)*Harvest + dTreeCover(2)*Harvest + dTertiaryRoads(2) + ElkProb*Harvest + DeerProb*Harvest	17	82246.01	4.62
E + S + W + Slope(2) + VRM(2)*Harvest(2) + dTreeCover(2)*Harvest + dTertiaryRoads(2):Harvest + ElkProb*Harvest + DeerProb*Harvest	18	82246.93	5.54
E + S + W + Slope(2) + VRM(2)*Harvest(2) + dTreeCover(2)*Harvest + dTertiaryRoads(2) + ElkProb*Harvest + DeerProb*Harvest	18	82248.45	7.06
E + S + W + Slope(2) + VRM*Harvest + dTreeCover(2)*Harvest + dTertiaryRoads(2) + ElkProb*Harvest + DeerProb*Harvest	16	82262.96	21.57
E + S + W + Slope(2) + VRM(2)*Harvest + dTreeCover(2)*Harvest + dTertiaryRoads(2) + ElkProb + DeerProb	15	82280.10	38.71
E + S + W + Slope(2) + VRM*Harvest + dTreeCover*Harvest + dTertiaryRoads(2) + ElkProb*Harvest + DeerProb*Harvest	15	82290.21	48.82
E + S + W + Slope(2) + VRM(2)*Active(2) + dTreeCover(2)+ dTertiaryRoads(2) + ElkProb + DeerProb	15	82290.81	49.42
E + S + W + Slope(2) + VRM(2)*Active(2) + dTreeCover(2)+ dTertiaryRoads(2) + ElkProb*Active + DeerProb*Active	17	82291.97	50.58
E + S + W + Slope(2) + VRM(2) + dTreeCover(2) + dTertiaryRoads(2) + ElkProb + DeerProb	13	82293.24	51.85
E + S + W + Slope(2) + VRM(2) + dist_roc(2) + dTreeCover(2) + dSprings(2) + dTertiaryRoads(2) + ElkProb(2) + DeerProb(2)	15	82296.84	55.45
E + S + W + Slope(2) + VRM*Active + dTreeCover(2)+ dTertiaryRoads(2) + ElkProb + DeerProb	13	82310.80	69.41
E + S + W + Slope(2) + VRM + dTreeCover(2) + dTertiaryRoads(2) + ElkProb + DeerProb	12	82311.60	70.21

TABLE C6. cont.

E + S + W + Slope(2) + VRM*Active + dTreeCover(2)+ dTertiaryRoads(2) + ElkProb*Active + DeerProb*Active	15	82311.92	70.53
E + S + W + Slope(2) + VRM(2) + dTreeCover + dTertiaryRoads(2) + ElkProb + DeerProb	12	82319.48	78.09
E + S + W + Slope(2) + VRM(2) + dist_roc(2) + dTreeCover(2) + dSprings(2) + dTertiaryRoads(2) + ElkProb + DeerProb	15	82323.39	82.00
E + S + W + Slope(2) + VRM*Active + dTreeCover*Active + dTertiaryRoads(2) + ElkProb*Active + DeerProb*Active	15	82338.27	96.88
E + S + W + Slope(2) + VRM*Harvest + dTreeCover*Harvest + dTertiaryRoads*Harvest + ElkProb*Harvest + DeerProb*Harvest	15	82349.55	108.16
E + S + W + Slope(2) + VRM(2) + dTreeCover(2) + dTertiaryRoads + ElkProb + DeerProb	12	82350.03	108.64
E + S + W + Slope(2) + VRM + dTreeCover(2) + dTertiaryRoads + ElkProb + DeerProb	11	82368.70	127.31
E + S + W + Slope(2) + VRM(2) + dTreeCover + dTertiaryRoads + ElkProb + DeerProb	11	82375.74	134.35
E + S + W + Slope(2) + VRM + dTreeCover + dTertiaryRoads + ElkProb + DeerProb	10	82394.54	153.15
E + S + W + Slope(2) + VRM*Active + dTreeCover*Active + dTertiaryRoads*Active + ElkProb*Active + DeerProb*Active	15	82394.86	153.47
E + S + W + Slope + VRM + dTreeCover + dTertiaryRoads + ElkProb + DeerProb	9	82580.25	338.86
E + S + W + Slope + VRM + dist_roc + dTreeCover + dTertiaryRoads + ElkProb + DeerProb	10	82595.48	354.09
E + S + W + Slope + VRM + dTreeCover + dTertiaryRoads	7	82597.17	355.78
E + S + W + Slope + VRM + dTreeCover + dSprings + dTertiaryRoads + ElkProb + DeerProb	10	82598.14	356.75

TABLE C6. cont.

E + S + W + Slope + VRM + dist_roc + dTreeCover + dSprings + dTertiaryRoads + ElkProb + DeerProb	11	82613.53	372.14
E + S + W + Slope + VRM + dTreeCover + ElkProb + DeerProb	8	82651.06	409.67
Slope + VRM + dist_roc + dTreeCover + dSprings + dTertiaryRoads + ElkProb + DeerProb	8	82679.19	437.80
E + S + W + dTreeCover + dTertiaryRoads + ElkProb + DeerProb	7	82855.32	613.93
E + S + W + dTreeCover + ElkProb + DeerProb	6	83000.45	759.06
E + S + W + Slope + VRM + dTertiaryRoads + ElkProb + DeerProb	8	83021.12	779.73
E + S + W + dTreeCover	4	83046.46	805.07
E + S + W + Slope + VRM + ElkProb + DeerProb	7	83106.98	865.59
E + S + W + VRM + ElkProb + DeerProb	6	83410.91	1169.52
E + S + W + VRM	4	83467.65	1226.26
ElkProb + DeerProb	2	83617.29	1375.90

APPENDIX D. CHAPTER 5 SUPPLEMENTARY TABLES AND FIGURES

Table D1. Summary statistics of potential predation clusters estimated from a single female cougar (F53) on Monroe Mountain, Fishlake National Forest.

				Proportion of fixes in:					
Cluster ID	**Duration (hours)**	**Number of Fixes**	**Area (km^2)**	**State 1**	**State 2**	**State 3**	**State 4**	**Night**	**Crepusc.**
1	13.4	5	230.22	1.00	0.00	0.00	0.00	0.60	0.00
2	12.0	4	843.63	0.50	0.50	0.00	0.00	0.75	0.00
3	8.0	3	1356.17	0.67	0.33	0.00	0.00	0.00	0.00
4	28.0	5	430.17	0.80	0.20	0.00	0.00	0.00	0.00
5	28.0	4	130.60	1.00	0.00	0.00	0.00	1.00	0.00
6	28.0	8	707.85	0.25	0.13	0.50	0.13	0.63	0.00
7	8.0	3	1358.45	0.67	0.33	0.00	0.00	0.00	0.00
8	8.0	3	44.40	0.67	0.33	0.00	0.00	0.00	0.00
9	96.0	4	628.64	0.25	0.25	0.25	0.25	1.00	0.00
10	8.0	3	13.99	0.67	0.33	0.00	0.00	0.00	0.00
11	32.0	6	72.36	0.33	0.50	0.00	0.17	0.00	0.00
12	52.0	4	1640.14	0.00	0.50	0.50	0.00	1.00	0.00
13	8.0	3	48.96	0.67	0.33	0.00	0.00	0.00	0.00
14	64.0	16	3191.93	0.50	0.19	0.25	0.06	0.50	0.00
15	8.0	3	532.13	0.33	0.33	0.00	0.33	0.00	0.00
16	60.0	11	2004.63	0.00	0.45	0.55	0.00	0.45	0.18
17	8.0	3	17.84	1.00	0.00	0.00	0.00	0.00	0.33
18	132.0	31	642.04	0.06	0.61	0.29	0.03	0.35	0.19
19	48.0	12	934.84	0.25	0.67	0.08	0.00	0.33	0.17
20	104.0	16	2901.99	0.13	0.44	0.38	0.06	0.44	0.13
21	8.0	3	102.11	0.67	0.00	0.00	0.33	0.67	0.33
22	36.0	7	1137.57	0.29	0.29	0.43	0.00	0.57	0.14
23	8.0	3	266.45	0.67	0.33	0.00	0.00	0.00	0.00
24	28.0	3	11.79	0.33	0.33	0.00	0.33	1.00	0.00
25	216.0	45	3178.43	0.20	0.58	0.22	0.00	0.36	0.13
26	76.0	11	5147.16	0.00	0.73	0.18	0.09	0.36	0.45
27	60.0	12	12676.13	0.58	0.25	0.00	0.17	0.08	0.25
28	24.0	5	284.53	0.20	0.60	0.20	0.00	0.00	0.40
29	32.0	8	3819.78	0.50	0.38	0.13	0.00	0.13	0.25
30	52.0	9	3110.09	0.67	0.22	0.11	0.00	0.11	0.22
31	24.0	3	350.32	0.33	0.33	0.33	0.00	0.00	0.00
32	12.0	4	31.58	0.25	0.75	0.00	0.00	0.25	0.50
33	72.0	8	839.68	0.63	0.13	0.25	0.00	0.13	0.38

Table D1. cont.

34	8.0	3	31.77	0.33	0.67	0.00	0.00	0.00	0.00
35	8.0	3	2.21	0.00	1.00	0.00	0.00	0.00	0.00
36	32.0	5	442.49	0.20	0.60	0.00	0.20	0.00	0.80
37	8.0	3	269.03	0.67	0.00	0.00	0.33	0.00	0.00
38	12.0	4	1168.36	1.00	0.00	0.00	0.00	0.25	0.25
39	68.0	10	328.22	0.20	0.60	0.20	0.00	0.30	0.50
40	52.0	5	250.69	0.40	0.60	0.00	0.00	0.00	0.00
41	20.0	3	70.70	0.00	0.33	0.00	0.67	0.33	0.33
42	36.0	9	2844.35	0.22	0.44	0.22	0.11	0.11	0.22
43	40.0	7	2633.82	0.14	0.43	0.29	0.14	0.00	0.43
44	68.0	4	4911.66	0.50	0.25	0.25	0.00	0.25	0.50
45	164.0	29	13446.57	0.21	0.62	0.10	0.07	0.21	0.31
46	56.0	4	1872.51	0.75	0.25	0.00	0.00	0.00	0.00
47	68.0	13	1792.32	0.38	0.23	0.31	0.08	0.23	0.38
48	16.0	5	681.00	0.40	0.20	0.40	0.00	0.20	0.20
49	108.0	23	6706.21	0.26	0.39	0.35	0.00	0.17	0.35
50	44.0	9	2621.19	0.33	0.22	0.44	0.00	0.22	0.44
51	8.0	3	77.97	1.00	0.00	0.00	0.00	0.00	0.00
52	96.0	10	3405.12	0.30	0.40	0.20	0.10	0.30	0.50
53	12.0	4	134.73	0.00	0.75	0.25	0.00	0.25	0.50
54	16.0	4	821.31	0.75	0.00	0.25	0.00	0.25	0.00
55	32.0	8	1070.50	0.38	0.50	0.13	0.00	0.13	0.13
56	72.0	8	5173.46	0.25	0.38	0.13	0.25	0.38	0.50
57	72.0	12	5749.57	0.00	0.83	0.08	0.08	0.17	0.50
58	8.0	3	213.16	0.67	0.33	0.00	0.00	0.00	0.00
59	48.0	9	463.31	0.22	0.33	0.44	0.00	0.11	0.56
60	48.0	6	282.16	0.50	0.50	0.00	0.00	0.33	0.67
61	72.0	16	2251.16	0.25	0.19	0.56	0.00	0.19	0.31
62	24.0	5	423.57	0.20	0.40	0.40	0.00	0.40	0.40
63	36.0	8	3637.05	0.25	0.50	0.25	0.00	0.50	0.13
64	8.0	3	322.98	0.67	0.33	0.00	0.00	0.00	0.00
65	216.0	47	12050.05	0.09	0.77	0.15	0.00	0.36	0.17
66	148.0	11	662.76	0.36	0.36	0.27	0.00	0.09	0.09
67	104.0	22	900.94	0.23	0.73	0.05	0.00	0.36	0.23
68	8.0	3	1020.76	0.33	0.33	0.33	0.00	0.67	0.33
69	136.0	23	13404.03	0.78	0.13	0.09	0.00	0.35	0.13
70	20.0	5	112.64	1.00	0.00	0.00	0.00	0.40	0.00
71	20.0	4	1004.60	0.75	0.25	0.00	0.00	0.25	0.00
72	32.0	3	158.90	0.67	0.33	0.00	0.00	0.67	0.33

Table D1. cont.

73	20.0	4	50.09	0.25	0.50	0.25	0.00	0.50	0.25
74	48.0	11	712.44	0.27	0.36	0.27	0.09	0.64	0.00
75	120.0	22	1909.59	0.09	0.73	0.09	0.09	0.64	0.00
76	60.0	3	2260.64	0.33	0.67	0.00	0.00	0.67	0.00
77	8.0	3	266.13	1.00	0.00	0.00	0.00	0.00	0.00
78	8.0	3	515.81	0.67	0.33	0.00	0.00	0.00	0.00
79	8.0	3	18.66	0.00	0.67	0.33	0.00	0.00	0.00
80	28.0	4	1724.31	0.25	0.25	0.25	0.25	1.00	0.00
81	120.0	15	209.50	0.33	0.20	0.33	0.13	0.60	0.00
82	92.0	4	2539.52	0.25	0.50	0.00	0.25	1.00	0.00
83	76.0	9	1649.69	0.11	0.33	0.33	0.22	0.78	0.00
84	28.0	5	265.86	0.80	0.20	0.00	0.00	0.00	0.00
85	8.0	3	35.12	0.67	0.33	0.00	0.00	0.00	0.00
86	8.0	3	192.00	0.67	0.00	0.00	0.33	0.00	0.00
87	128.0	27	2438.43	0.22	0.52	0.26	0.00	0.63	0.00
88	44.0	4	3081.13	0.25	0.50	0.25	0.00	0.00	0.00
89	8.0	3	608.78	0.33	0.33	0.00	0.33	0.00	0.00

Table D2. Observed versus predicted kill species at cougar clusters as estimated using random forest with 17 predictor variables. The Other category represents a single beaver, coyote, and domestic cow, as well as two domestic sheep.

		Predicted		
		Mule Deer	*Elk*	*Other*
Observed	*Mule Deer*	38	4	0
	Elk	11	11	0
	Other	5	0	0

Table D3. Cluster point summary statistics from an assessment of den and rendezvous site selection in a high-elevation pack (C028) on Monroe Mountain, Fishlake National Forest, Utah.

					Raw Activity (Dual Axis Acceler.)		Composite Activity			BCPA Statistics		
Point ID	**Elevation (m)**	**Date/Time**	**Cluster ID**	**Diurnal Period**	**X**	**Y**	**VeDBA**	**ODBA**	**Behaviour State**	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\tau}$
1123	3024.27	5/14/14 23:01	1	Day	22	34	40.50	56.00	1	65.44	67.91	7.44
1127	2969.15	5/16/14 15:01	1	Day	0	0	0.00	0.00	1	25.79	36.94	9.03
1132	3005.98	5/18/14 15:02	1	Day	0	0	0.00	0.00	1	0.10	0.48	0.47
1135	2978.17	5/19/14 15:01	1	Day	0	0	0.00	0.00	1	10.06	21.32	4.34
1136	2975.12	5/19/14 23:01	1	Day	32	34	46.69	66.00	1	70.94	74.90	10.35
1138	3040.07	5/20/14 15:01	1	Day	3	0	3.00	3.00	1	22.78	20.41	8.01
1142	2994.43	5/22/14 23:03	1	Day	46	60	75.60	106.00	1	127.44	73.46	8.94
1144	2915.27	5/23/14 23:02	1	Day	9	8	12.04	17.00	2	88.76	65.33	16.42
1145	2911.76	5/24/14 7:02	1	Night	9	20	21.93	29.00	1	118.70	87.07	10.19
1150	2929.4	5/26/14 23:01	1	Day	0	0	0.00	0.00	1	3.94	9.03	4.92
1155	2977.32	5/28/14 15:02	1	Day	0	0	0.00	0.00	1	52.99	44.06	9.27
1162	2867.63	5/31/14 15:02	1	Day	0	0	0.00	0.00	1	5.14	9.25	3.27
1165	2806.3	6/1/14 13:01	1	Day	0	0	0.00	0.00	1	0.29	0.83	2.32
1168	2994.67	6/2/14 1:02	1	Day	0	0	0.00	0.00	1	0.32	0.84	1.47

Table D3. cont.

1169	3036.46	6/2/14 4:01	1	Dusk	0	0	0.00	0.00	1	51.88	49.46	8.47
1172	3058.11	6/2/14 19:01	1	Day	29	36	46.23	65.00	1	82.26	81.37	7.19
1173	3052.14	6/2/14 22:02	2	Day	0	0	0.00	0.00	1	3.08	6.20	4.08
1176	3029.52	6/3/14 10:01	2	Night	0	0	0.00	0.00	1	1.11	2.91	3.19
1177	3035.27	6/3/14 13:01	2	Day	0	0	0.00	0.00	1	0.83	2.71	0.99
1178	3033.88	6/3/14 16:02	2	Day	0	0	0.00	0.00	1	0.44	1.57	0.46
1179	3011.14	6/3/14 19:01	2	Day	3	5	5.83	8.00	1	71.71	44.31	7.26
1185	2997	6/4/14 13:02	2	Day	0	0	0.00	0.00	1	1.70	4.75	2.50
1186	3006.95	6/4/14 16:02	2	Day	0	0	0.00	0.00	1	0.03	0.13	3.65
1187	3011.22	6/4/14 19:01	2	Day	0	0	0.00	0.00	1	5.23	6.96	2.48
1188	3011.49	6/4/14 22:01	2	Day	0	0	0.00	0.00	1	1.32	4.22	4.67
1193	2945.12	6/5/14 13:01	2	Day	0	0	0.00	0.00	1	37.17	29.75	8.85
1194	2944.98	6/5/14 16:01	2	Day	0	0	0.00	0.00	1	73.75	80.83	10.00
1196	2991.32	6/5/14 22:01	2	Day	0	0	0.00	0.00	1	0.01	0.05	0.55
1197	2994.64	6/6/14 1:01	2	Day	0	0	0.00	0.00	1	0.12	0.49	0.86
1200	2921.25	6/6/14 13:02	2	Day	0	0	0.00	0.00	1	121.32	96.00	36.62
1203	3013.03	6/6/14 22:01	2	Day	34	39	51.74	73.00	1	41.55	46.80	9.22
1205	3203.23	6/7/14 7:01	2	Night	0	0	0.00	0.00	1	0.11	0.62	0.57
1208	2990.6	6/7/14 16:02	2	Day	0	0	0.00	0.00	1	7.63	12.31	1.74

Table D3. cont.

1212	2996.51	6/8/14 4:01	2	Dusk	36	45	57.63	81.00	2	10.44	21.38	3.33
1218	2865.97	6/9/14 4:03	2	Dusk	0	0	0.00	0.00	1	0.19	0.78	0.55
1219	2990.92	6/9/14 7:01	2	Night	44	49	65.86	93.00	1	27.93	41.24	8.15
1224	2988.16	6/9/14 22:01	2	Day	0	0	0.00	0.00	1	9.59	16.68	4.95
1225	3017.02	6/10/14 10:02	2	Night	0	0	0.00	0.00	1	0.28	1.02	1.74
1226	3016.47	6/10/14 13:02	2	Day	2	0	2.00	2.00	1	1.16	3.82	2.87
1228	3017.62	6/10/14 19:01	2	Day	0	0	0.00	0.00	1	0.29	0.93	0.12
1229	3016.96	6/10/14 22:01	2	Day	95	87	128.82	182.00	1	40.54	58.46	4.36
1231	3014.39	6/11/14 4:03	2	Dusk	0	0	0.00	0.00	1	54.90	47.14	5.31
1237	3014.89	6/11/14 22:01	2	Day	0	0	0.00	0.00	1	19.26	20.82	5.47
1238	3013.31	6/12/14 1:02	2	Day	0	0	0.00	0.00	1	31.07	36.01	13.63
1242	3002.99	6/12/14 13:01	2	Day	1	1	1.41	2.00	1	1.64	5.28	0.51
1243	3005.21	6/12/14 16:01	2	Day	0	0	0.00	0.00	1	0.46	1.31	0.49
1244	3002.39	6/12/14 19:01	2	Day	0	0	0.00	0.00	1	0.46	1.71	2.98
1246	3029.88	6/13/14 4:01	2	Dusk	0	0	0.00	0.00	1	10.26	15.81	9.78
1250	2875.45	6/13/14 16:03	2	Day	0	0	0.00	0.00	1	0.06	0.19	0.18
1251	2882.1	6/13/14 19:01	2	Day	2	3	3.61	5.00	1	0.87	2.38	0.27
1252	2881.42	6/13/14 22:01	2	Day	0	0	0.00	0.00	2	52.72	39.29	8.23
1255	3154.58	6/14/14 7:01	2	Night	26	25	36.07	51.00	1	107.71	89.02	32.68

Table D3. cont.

1256	3021.84	6/14/14 10:01	2	Night	0	0	0.00	0.00	1	7.98	11.05	3.77
1258	2983.55	6/14/14 16:02	2	Day	0	0	0.00	0.00	1	0.74	2.73	2.16
1258	2983.55	6/14/14 16:02	2	Day	0	0	0.00	0.00	1	0.44	1.75	2.16
1258	2983.55	6/14/14 16:02	2	Day	0	0	0.00	0.00	1	0.74	2.73	2.16
1258	2983.55	6/14/14 16:02	2	Day	0	0	0.00	0.00	1	0.44	1.75	2.16
1259	3025.32	6/14/14 22:02	2	Day	74	88	114.98	162.00	1	86.70	60.84	22.46
1276	3029.02	6/17/14 10:00	2	Night	0	0	0.00	0.00	1	52.93	45.22	13.14
1280	2781.98	6/18/14 4:01	2	Dusk	197	189	273.00	386.00	1	130.26	81.23	10.71
1311	2958.04	6/23/14 13:02	2	Day	0	0	0.00	0.00	1	0.03	0.16	0.65
1344	3128.67	6/30/14 19:02	2	Day	0	0	0.00	0.00	1	9.06	8.69	1.76
1257	3024.53	6/14/14 13:01	3	Day	0	0	0.00	0.00	3	0.64	2.14	1.39
1261	3092.41	6/15/14 7:03	3	Night	137	113	177.59	250.00	2	112.06	79.14	15.80
1263	3089.16	6/15/14 16:02	3	Day	0	0	0.00	0.00	1	10.18	20.64	2.83
1264	3082.38	6/15/14 19:01	3	Day	0	0	0.00	0.00	3	0.31	1.08	2.29
1265	3083.74	6/15/14 22:02	3	Day	0	0	0.00	0.00	3	1.68	4.61	1.65
1266	3123.51	6/16/14 1:02	3	Day	0	0	0.00	0.00	1	15.10	23.83	4.13
1266	3123.51	6/16/14 1:02	3	Day	0	0	0.00	0.00	1	17.81	27.37	4.63
1266	3123.51	6/16/14 1:02	3	Day	0	0	0.00	0.00	1	15.10	23.83	4.13
1266	3123.51	6/16/14 1:02	3	Day	0	0	0.00	0.00	1	17.81	27.37	4.63

Table D3. cont.

1268	3127.96	6/16/14 7:02	3	Night	7	10	12.21	17.00	1	57.31	67.61	18.37
1269	3124.2	6/16/14 10:02	3	Night	0	0	0.00	0.00	3	10.37	19.50	4.40
1277	3077.52	6/17/14 16:02	4	Day	13	8	15.26	21.00	3	2.21	5.31	0.80
1278	3074.86	6/17/14 19:01	4	Day	0	0	0.00	0.00	3	1.22	3.31	1.53
1283	3042.86	6/18/14 13:01	4	Day	0	0	0.00	0.00	1	0.60	1.92	2.35
1286	3035.51	6/18/14 22:01	4	Day	0	0	0.00	0.00	1	39.50	40.83	7.22
1287	3037.69	6/19/14 1:01	4	Day	0	0	0.00	0.00	3	0.53	1.49	0.61
1288	3071.49	6/19/14 4:01	4	Dusk	0	0	0.00	0.00	2	36.93	42.55	6.30
1289	3078.24	6/19/14 13:02	4	Day	0	0	0.00	0.00	3	19.68	29.64	10.37
1249	2876.53	6/13/14 13:01	5	Day	1	0	1.00	1.00	3	8.16	14.19	3.65
1293	3024.07	6/20/14 4:03	5	Dusk	0	0	0.00	0.00	1	5.74	6.85	5.13
1294	3026.28	6/20/14 7:02	5	Night	0	0	0.00	0.00	1	14.25	20.24	4.06
1295	3025.84	6/20/14 13:02	5	Day	0	0	0.00	0.00	1	0.05	0.26	2.72
1304	2945.21	6/22/14 1:02	5	Day	0	0	0.00	0.00	1	0.50	1.26	0.49
1307	2982.35	6/22/14 10:02	5	Night	0	0	0.00	0.00	1	0.09	0.37	2.53
1308	2982.87	6/22/14 16:02	5	Day	20	22	29.73	42.00	3	5.09	11.83	0.79
1308	2982.87	6/22/14 16:02	5	Day	20	22	29.73	42.00	3	5.05	11.81	0.79
1308	2982.87	6/22/14 16:02	5	Day	0	0	0.00	0.00	3	5.09	11.83	0.79
1308	2982.87	6/22/14 16:02	5	Day	0	0	0.00	0.00	3	5.05	11.81	0.79

Table D3. cont.

1309	3008.29	6/22/14 19:01	5	Day	0	0	0.00	0.00	3	1.12	4.88	1.92
1313	2989.36	6/24/14 4:01	5	Dusk	0	0	0.00	0.00	1	6.40	13.89	10.54
1314	2988.61	6/24/14 7:00	5	Night	0	0	0.00	0.00	1	6.53	16.49	3.94
1315	3010.39	6/24/14 10:02	5	Night	2	0	2.00	2.00	1	21.41	29.32	10.39
1316	2979.4	6/24/14 16:01	5	Day	0	0	0.00	0.00	1	2.63	5.84	4.60
1317	2977.66	6/24/14 19:01	5	Day	0	0	0.00	0.00	1	1.53	4.25	1.02
1318	2997.37	6/25/14 1:01	5	Day	17	20	26.25	37.00	1	205.99	111.94	18.12
1319	3031.79	6/25/14 7:01	5	Night	6	5	7.81	11.00	1	8.40	15.60	3.15
1321	3021.57	6/25/14 19:01	5	Day	0	0	0.00	0.00	3	2.87	7.94	3.32
1322	3000.05	6/26/14 1:00	5	Day	155	128	201.02	283.00	3	125.65	78.17	8.64
1323	3000.47	6/26/14 4:02	5	Dusk	0	0	0.00	0.00	3	15.81	30.08	8.23
1326	3091.59	6/26/14 19:01	5	Day	1	0	1.00	1.00	1	8.13	12.58	5.09
1328	3009.97	6/27/14 13:03	5	Day	0	0	0.00	0.00	1	4.43	6.06	1.84
1329	3009.54	6/27/14 19:03	5	Day	13	16	20.62	29.00	1	124.01	92.34	14.07
1330	3026.51	6/28/14 1:01	5	Day	0	0	0.00	0.00	1	3.30	7.69	3.38
1331	3014.96	6/28/14 4:01	5	Dusk	0	0	0.00	0.00	1	2.93	6.82	2.85
1333	3038.4	6/28/14 13:03	5	Day	80	97	125.73	177.00	2	122.74	79.39	10.70
1334	3034.1	6/28/14 16:01	5	Day	16	20	25.61	36.00	1	22.80	36.14	5.59
1335	3036.46	6/28/14 19:03	5	Day	0	0	0.00	0.00	1	0.80	2.33	0.93

Table D3. cont.

1337	3008.08	6/29/14 4:03	5	Dusk	0	0	0.00	0.00	1	0.00	0.00	0.12
1339	3026.41	6/29/14 16:01	5	Day	0	0	0.00	0.00	1	85.70	81.79	11.94
1342	3150.71	6/30/14 10:01	5	Night	0	0	0.00	0.00	1	1.09	2.26	5.02
1343	3125.86	6/30/14 13:01	5	Day	0	0	0.00	0.00	1	25.94	22.08	10.84
1345	3125.8	6/30/14 22:03	5	Day	0	0	0.00	0.00	1	0.31	1.07	0.20
1346	3024.02	7/1/14 1:00	5	Day	15	14	20.52	29.00	2	48.35	45.66	4.58
1347	3024.42	7/1/14 10:01	5	Night	0	0	0.00	0.00	3	1.86	6.62	1.66
1351	2996.23	7/2/14 1:01	5	Day	0	0	0.00	0.00	1	0.79	2.21	0.27
1352	3005.31	7/2/14 4:01	5	Dusk	0	0	0.00	0.00	1	12.19	25.23	8.96
1354	3012.87	7/2/14 10:02	5	Night	0	0	0.00	0.00	1	13.55	11.73	5.53
1358	3086.46	7/3/14 4:01	5	Dusk	17	16	23.35	33.00	1	7.26	16.68	4.25
1359	3026.93	7/3/14 7:00	5	Night	0	0	0.00	0.00	3	0.14	0.53	1.10
1364	2910.34	7/4/14 1:01	5	Day	49	70	85.45	119.00	1	18.20	31.44	4.30
1325	3103.9	6/26/14 16:03	6	Day	73	75	104.66	148.00	1	129.85	74.36	5.55
1370	3075.11	7/5/14 7:01	6	Night	0	0	0.00	0.00	1	0.02	0.09	0.42
1373	3124.4	7/5/14 22:02	6	Day	0	0	0.00	0.00	1	0.08	0.27	0.37
1374	3120.41	7/6/14 1:02	6	Day	0	0	0.00	0.00	1	9.24	20.33	4.61
1376	3116.89	7/6/14 10:02	6	Night	0	0	0.00	0.00	1	3.02	3.79	3.33
1376	3116.89	7/6/14 10:02	6	Night	0	0	0.00	0.00	1	0.00	0.00	2.05

Table D3. cont.

1376	3116.89	7/6/14 10:02	6	Night	0	0	0.00	0.00	1	3.02	3.79	3.33
1376	3116.89	7/6/14 10:02	6	Night	0	0	0.00	0.00	1	0.00	0.00	2.05
1377	3117.96	7/6/14 13:03	6	Day	0	0	0.00	0.00	1	0.30	1.07	0.27
1381	3003.11	7/7/14 1:02	6	Day	0	0	0.00	0.00	2	17.08	32.08	10.32
1384	2951.36	7/7/14 13:02	6	Day	0	0	0.00	0.00	1	1.59	4.17	1.75
1387	3082.1	7/7/14 22:02	6	Day	0	0	0.00	0.00	1	41.49	54.40	17.48
1387	3082.1	7/7/14 22:02	6	Day	0	0	0.00	0.00	1	41.92	55.53	17.42
1387	3082.1	7/7/14 22:02	6	Day	1	0	1.00	1.00	1	41.49	54.40	17.48
1387	3082.1	7/7/14 22:02	6	Day	1	0	1.00	1.00	1	41.92	55.53	17.42
1388	3083.49	7/8/14 7:01	6	Night	0	0	0.00	0.00	1	27.42	42.45	3.77
1390	3080.95	7/8/14 13:01	6	Day	115	106	156.40	221.00	1	77.51	52.49	3.33
1393	3085.18	7/9/14 4:02	6	Dusk	0	0	0.00	0.00	1	1.58	4.44	0.71
1397	2972.64	7/9/14 16:02	6	Day	84	89	122.38	173.00	1	27.60	39.90	3.38
1399	3065.6	7/9/14 22:01	6	Day	3	1	3.16	4.00	1	18.55	31.85	5.81
1403	3027.5	7/10/14 10:02	6	Night	0	0	0.00	0.00	1	22.74	38.40	7.05
1404	3148.03	7/10/14 13:02	6	Day	0	0	0.00	0.00	1	0.00	0.01	1.94
1405	3088.74	7/10/14 16:00	6	Day	0	0	0.00	0.00	1	57.21	40.77	7.12
1407	3067.35	7/11/14 4:02	6	Dusk	0	0	0.00	0.00	1	1.20	4.76	1.13
1409	2990.23	7/11/14 13:02	6	Day	0	0	0.00	0.00	1	0.08	0.28	0.25

Table D3. cont.

1410	2989.91	7/11/14 22:01	6	Day	0	0	0.00	0.00	1	2.40	6.71	1.07
1412	2817.61	7/12/14 7:01	6	Night	27	22	34.83	49.00	1	44.02	61.79	9.69
1415	3057.98	7/12/14 19:01	6	Day	0	0	0.00	0.00	1	0.35	1.05	0.32
1417	3058.72	7/13/14 4:01	6	Dusk	1	0	1.00	1.00	1	21.87	37.41	9.82
1428	2798.88	7/14/14 19:03	6	Day	0	0	0.00	0.00	1	0.47	1.25	1.04
1433	3062.14	7/15/14 10:01	6	Night	0	0	0.00	0.00	1	8.98	21.46	6.90
1434	3054.99	7/15/14 13:01	6	Day	0	0	0.00	0.00	1	0.05	0.19	0.41
1443	3003.21	7/17/14 4:02	6	Dusk	0	0	0.00	0.00	1	0.00	0.01	2.68
1497	3096.44	7/25/14 7:01	6	Night	0	0	0.00	0.00	1	0.70	1.88	0.55
1367	3067.17	7/4/14 22:01	7	Day	0	0	0.00	0.00	1	1.33	4.25	0.13
1368	3065.25	7/5/14 1:01	7	Day	0	0	0.00	0.00	3	0.12	0.50	0.45
1383	2954.71	7/7/14 10:01	7	Night	0	0	0.00	0.00	1	0.50	1.57	0.50
1389	3082.48	7/8/14 10:01	7	Night	0	0	0.00	0.00	2	1.98	2.75	2.50
1431	3082.77	7/15/14 4:01	7	Dusk	0	0	0.00	0.00	1	11.11	14.70	9.15
1435	3056	7/15/14 22:01	7	Day	0	0	0.00	0.00	1	36.73	48.51	17.95
1438	3078.04	7/16/14 7:01	7	Night	19	16	24.84	35.00	1	45.62	63.12	13.30
1439	3074.5	7/16/14 10:01	7	Night	0	0	0.00	0.00	1	0.40	0.93	2.94
1440	3086.28	7/16/14 13:02	7	Day	0	0	0.00	0.00	1	0.37	1.30	1.32
1458	3168.6	7/19/14 4:03	7	Dusk	0	0	0.00	0.00	1	59.73	47.73	10.57

Table D3. cont.

1459	3154.26	7/19/14 7:02	7	Night	0	0	0.00	0.00	1	1.18	3.70	1.27
1460	3085.19	7/19/14 10:01	7	Night	0	0	0.00	0.00	1	1.02	2.78	0.93
1461	3083.81	7/19/14 13:01	7	Day	0	0	0.00	0.00	1	24.81	24.60	4.65
1482	2799.82	7/23/14 4:03	7	Dusk	88	105	137.00	193.00	1	155.35	95.65	16.32
1486	3089.42	7/23/14 19:01	7	Day	1	0	1.00	1.00	1	73.12	72.95	28.95
1493	3115.99	7/24/14 19:01	7	Day	0	0	0.00	0.00	3	2.01	6.60	1.19
1501	3033.45	7/25/14 19:01	7	Day	0	0	0.00	0.00	2	79.11	96.37	13.71
1508	3087.54	7/26/14 19:01	7	Day	0	0	0.00	0.00	1	5.36	10.28	4.67
1429	3063.68	7/14/14 22:01	8	Day	0	0	0.00	0.00	1	16.27	39.94	5.89
1470	2904.83	7/20/14 16:01	8	Day	0	0	0.00	0.00	1	29.58	31.29	9.92
1488	3166.12	7/24/14 1:01	8	Day	25	27	36.80	52.00	1	102.96	72.18	19.56
1489	3171.92	7/24/14 4:02	8	Dusk	0	0	0.00	0.00	1	5.63	11.23	3.98
1490	3103.51	7/24/14 7:00	8	Night	0	0	0.00	0.00	1	31.66	31.30	5.59
1498	3095.07	7/25/14 10:03	8	Night	0	0	0.00	0.00	1	2.14	4.82	4.53
1516	3082.45	7/28/14 1:01	8	Day	0	0	0.00	0.00	1	133.65	119.65	30.55
1518	3074.79	7/28/14 7:03	8	Night	0	0	0.00	0.00	1	11.59	15.26	4.86
1519	3127.92	7/28/14 10:03	8	Night	0	0	0.00	0.00	1	0.27	0.85	2.30
1525	3072.22	7/29/14 16:01	8	Day	0	0	0.00	0.00	1	0.71	1.98	0.79
1530	2962.32	7/30/14 10:03	8	Night	0	0	0.00	0.00	1	4.12	9.36	1.84

Table D3. cont.

1537	2864.19	7/31/14 10:02	8	Night	0	0	0.00	0.00	3	0.00	0.01	0.12
1465	2933.8	7/20/14 1:00	9	Day	0	0	0.00	0.00	1	0.03	0.12	0.92
1466	2897.12	7/20/14 4:01	9	Dusk	0	0	0.00	0.00	1	0.01	0.06	3.24
1468	2841.91	7/20/14 10:03	9	Night	0	0	0.00	0.00	1	16.70	28.29	4.81
1473	3211.45	7/21/14 13:02	9	Day	7	4	8.06	11.00	1	93.34	93.71	18.30
1474	3207.3	7/21/14 16:01	9	Day	0	0	0.00	0.00	1	0.04	0.15	1.20
1477	2888.48	7/22/14 7:01	9	Night	0	0	0.00	0.00	1	21.34	40.81	9.14
1491	3107.44	7/24/14 13:00	10	Day	0	0	0.00	0.00	3	40.43	52.52	7.33
1495	3089.98	7/25/14 1:01	10	Day	0	0	0.00	0.00	3	126.83	84.06	10.69
1496	3097.93	7/25/14 4:01	10	Dusk	0	0	0.00	0.00	3	3.36	9.39	4.13
1529	2962.91	7/30/14 7:02	10	Night	0	0	0.00	0.00	1	0.16	0.72	0.33
1531	2960.62	7/30/14 13:01	10	Day	0	0	0.00	0.00	3	17.54	19.06	3.55
1563	3027.74	8/10/14 15:01	11	Day	0	0	0.00	0.00	1	3.15	6.20	4.72
1565	3026.26	8/11/14 15:01	11	Day	0	0	0.00	0.00	3	2.64	5.98	4.55
1569	3031.5	8/12/14 23:01	11	Day	0	0	0.00	0.00	1	89.28	84.15	14.33
1572	2969.94	8/13/14 23:02	11	Day	0	0	0.00	0.00	3	3.67	7.22	3.78
1573	2969.05	8/14/14 7:03	11	Night	15	18	23.43	33.00	3	62.12	60.82	3.20
1574	2973.32	8/14/14 15:01	11	Day	73	106	128.71	179.00	2	122.38	110.39	12.41
1585	3012.59	8/19/14 15:01	12	Day	0	0	0.00	0.00	1	4.66	11.79	3.49

Table D3. cont.

1586	3011.98	8/20/14 7:03	12	Night	0	0	0.00	0.00	1	0.04	0.21	1.51
1587	3011.7	8/20/14 15:03	12	Day	0	0	0.00	0.00	3	5.29	10.56	4.14
1589	3019.8	8/21/14 7:02	12	Night	0	0	0.00	0.00	1	9.54	25.87	2.59
1594	3036.11	8/23/14 15:03	12	Day	68	68	96.17	136.00	1	98.33	47.41	24.61
1595	3029.04	8/23/14 23:02	12	Day	0	0	0.00	0.00	1	0.52	1.38	1.11
1603	2903.08	8/27/14 7:02	12	Night	0	0	0.00	0.00	3	24.49	45.13	6.46

Table D4. Home range overlap indices based on proportion of area overlap for all kernel density estimates and concave hull territories.

	KDE 95% Isopleth		**KDE 99% Isopleth**		**Concave Hull 100% Isopleth**	
Season	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Winter	0.035	0.020	0.145	0.065	0.002	0.003
Spring/Summer	0.018	0.019	0.126	0.066	0.003	0.004
Overall	0.030	0.021	0.139	0.066	0.003	0.004

Table D5. Three home range overlap indices for all kernel density estimates.

	KDE 95% Isopleth		**KDE 99% Isopleth**		**% Volume**	
Overlap Index	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Winter						
Proportion of Area	0.035	0.020	0.145	0.065	-	-
Probability of Encounter	0.020	0.009	0.076	0.084	-	-
Volume of Intersection	-	-	-	-	0.018	0.014
Spring/Summer						
Proportion of Area	0.018	0.019	0.126	0.066	-	-
Probability of Encounter	0.017	0.018	0.072	0.069	-	-
Volume of Intersection	-	-	-	-	0.022	0.016
Overall						
Proportion of Area	0.030	0.021	0.139	0.066	-	-
Probability of Encounter	0.019	0.012	0.074	0.077	-	-
Volume of Intersection	-	-	-	-	0.019	0.014

Table D6. Concave hull gap distances (in meters) for all known territorial boundaries.

Boundary	Median	Mean	SD
A	247.07	274.31	160.22
B	0.00	51.96	77.03
C	161.96	216.84	93.60
D	739.88	822.73	266.63
E	505.79	546.75	416.60
F	192.59	246.83	282.22
G	307.88	359.90	216.05
Overall	244.56	253.16	118.74

Table D7. Percentage of the estimated KDE utilization distribution volume within predicted territories.

	Mean	SD
Winter	0.928	0.019
Spring/Summer	0.869	0.071
Overall	0.898	0.060

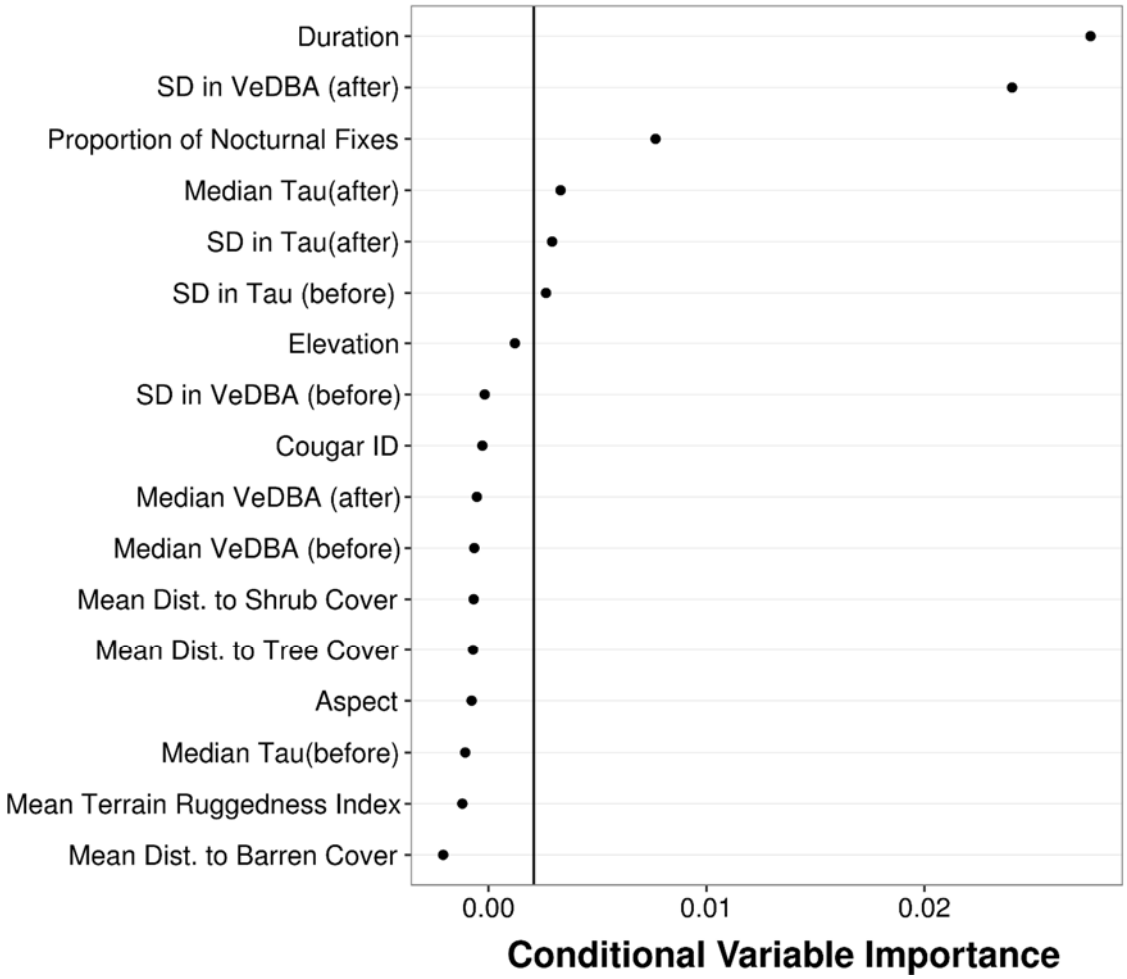

Figure D1. Conditional variable importance metrics for all 17 parameters in a random forest predictive model for cougar prey species. The vertical line is an importance threshold derived from the absolute value of the most negative variable importance metric. Values greater than this line correspond to influential variables.

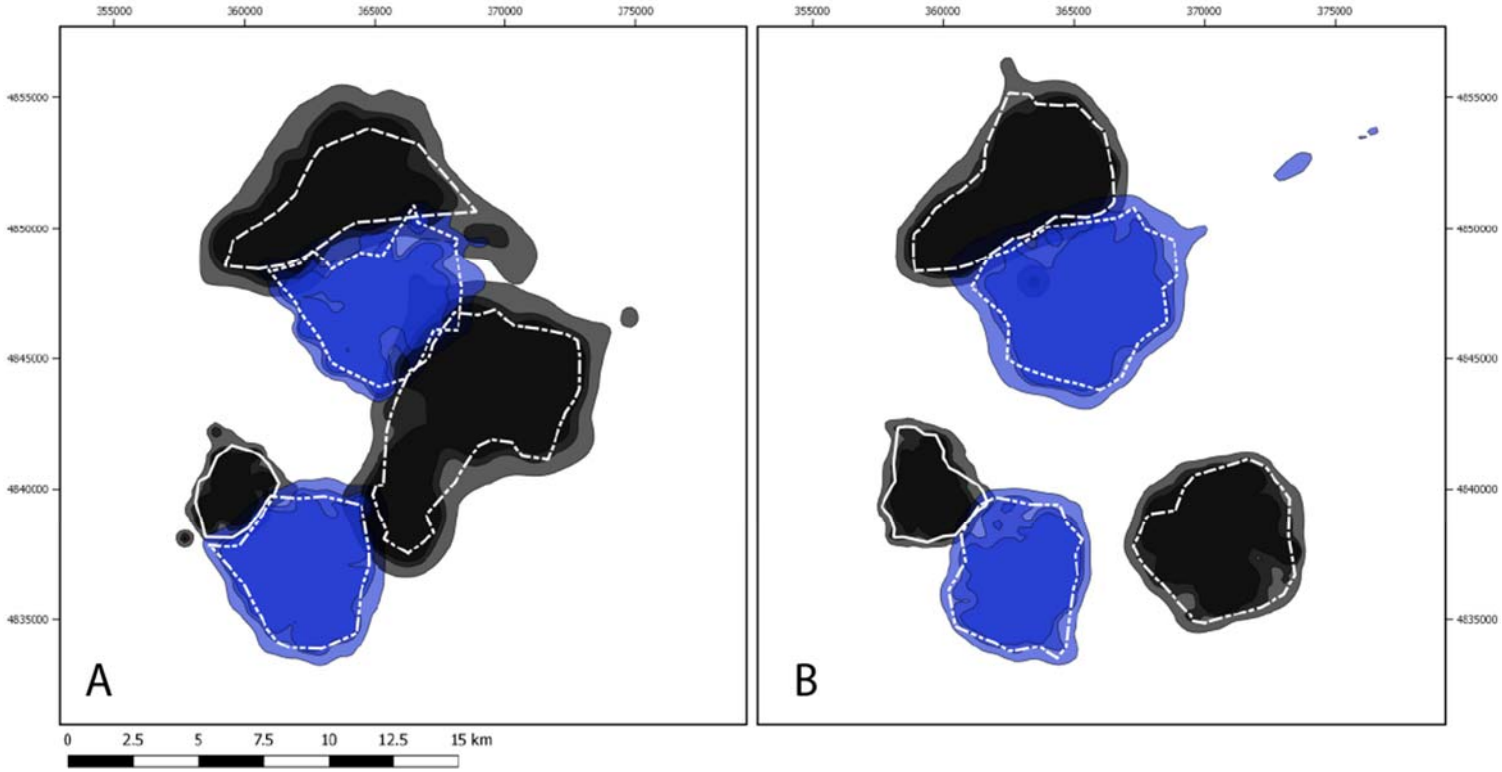

Figure D2. Home ranges for neighbouring packs during the winter (A) and spring/summer (B) of 2005. The semi-opaque kernel density estimates correspond to the 99%, 95%, and 90% isopleths (light to dark). The white lines correspond to the territory boundaries identified by site fidelity patterns using the clustering software.

APPENDIX E. PERMISSION LETTERS

Journal: Methods in Ecology and Evolution
Publisher: British Ecological Society

Hi Peter,

Thank you for your email. The license agreement that you signed after your article was accepted grants you permission to use the paper as part of your dissertation, as long as it is less than half of the whole dissertation. The relevant section of the agreement is in section C3b (I have copied this section below for your convenience).

If Utah State University required you to have signed permission from the journal, just let me know and I will fill out the form that you attached to your email.

If you have any questions, or if there is anything more that I can do to help, please let me know.

Best wishes,
Chris

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Chris Grieves
Assistant Editor – Methods in Ecology and Evolution

British Ecological Society
T: +44(0)207 685 2500
britishecologicalsociety.org

February 7, 2017

David Stoner, PhD
Dept. of Wildland Resources
Utah State University
5200 Old Main Hill
Logan, UT
84322

Dear Dr. David Stoner,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I am officially requesting your permission to use your mule deer (*Odocoileus hemionus*) location data set derived from global positioning system collars with funding from the NASA Biodiversity and Ecological Forecasting Program (Climate and Biological Responses, grant no. NNH10ZDA001N).

I will acknowledge you and your funders as a data source where appropriate and will include this letter as a special appendix. In addition, you will be granted co-authorship for Chapters II – IV pending your approval prior to submission for peer-review. Please inform me of any requested changes to the above. If what I have described is suitably, please approve my request by signing in the space provided.

Sincerely,

Peter J. Mahoney
peter.mahoney@aggiemail.usu.edu

I, David Stoner, hereby give permission to Peter J. Mahoney to use the aforementioned data in his dissertation.

Signed: _____

February 7, 2017

Kent Hersey
Big Game Project Leader
Utah Division of Wildlife Resources
1594 W. N. Temple
Salt Lake City, UT
84116

Dear Mr. Kent Hersey,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I am officially requesting your permission to use your mule deer (*Odocoileus hemionus*) location data set derived from global positioning system collars with funding from the Utah Division of Wildlife Resources.

I will acknowledge you and your agency as a data source where appropriate and will include this letter as a special appendix. In addition, you will be granted co-authorship for Chapter II pending your approval prior to submission for peer-review. Please inform me of any requested changes to the above. If what I have described is suitably, please approve my request by signing in the space provided.

Sincerely,

Peter J. Mahoney
peter.mahoney@aggiemail.usu.edu

I, Kent Hersey, hereby give permission to Peter J. Mahoney to use the aforementioned data in his dissertation.

Signed: _____

March 2, 2017

Randy Larsen, PhD
College of Life Sciences
Brigham Young University
5046 LSB
Provo, UT
84602

Dear Dr. Randy Larsen,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I am officially requesting your permission to use your mule deer (*Odocoileus hemionus*) location data set derived from global positioning system collars with funding from the Utah Division of Wildlife Resources.

I will acknowledge you and your funders as a data source where appropriate and will include this letter as a special appendix. In addition, you will be granted co-authorship for Chapters II – IV pending your approval prior to submission for peer-review. Please inform me of any requested changes to the above. If what I have described is suitably, please approve my request by signing in the space provided.

Sincerely,

Peter J. Mahoney
peter.mahoney@aggiemail.usu.edu

I, Randy Larsen, hereby give permission to Peter J. Mahoney to use the aforementioned data in his dissertation.

Signed: _____

March 2, 2017

Brock McMillan, PhD
College of Life Sciences
Brigham Young University
4105B LSB
Provo, UT
84602

Dear Dr. Brock McMillan,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I am officially requesting your permission to use your mule deer (*Odocoileus hemionus*) location data set derived from global positioning system collars with funding from the Utah Division of Wildlife Resources.

I will acknowledge you and your funders as a data source where appropriate and will include this letter as a special appendix. In addition, you will be granted co-authorship for Chapters II – IV pending your approval prior to submission for peer-review. Please inform me of any requested changes to the above. If what I have described is suitably, please approve my request by signing in the space provided.

Sincerely,

Peter J. Mahoney
peter.mahoney@aggiemail.usu.edu

I, Brock McMillan, hereby give permission to Peter J. Mahoney to use the aforementioned data in his dissertation.

Signed: _____

APPENDIX F. CURRICULUM VITAE

PETER J. MAHONEY

E-mail: pmahoney29@gmail.com
Website : http://pmahoney29@github.io

EDUCATION

Pres. **Ph.D. Candidate in Ecology**
Utah State University, Logan, UT
Department of Wildland Resources and the Ecology Center
GPA – 4.0

2011 **M.S. Wildlife Sciences**
Auburn University, Auburn, AL
School of Forestry and Wildlife Sciences
GPA – 4.0

2001 **B.A. Biology**
New College of Florida, Sarasota, FL
Division of Natural Sciences
GPA – 4.0 (equivalent)

PEER-REVIEWED PUBLICATIONS

Mahoney, P.J. and J.K. Young. 2016. Uncovering behavioral states by integrating site fidelity and activity. *Methods in Ecology and Evolution*.

Benson, J.F., **P.J. Mahoney**, J.A. Sikich, L.E.K. Serieys, J.P. Pollinger, H.B. Ernest, and S.P.D. Riley. 2016. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. *Proceedings of the Royal Society of London B* 283:20160957.

Tingley, R., **P.J. Mahoney**, K.H. Beard, A.M. Durso, *et al.* 2016. Extinction and invasion success in reptiles, are they two sides of the same coin? *Global Ecology and Biogeography*.

Benson, J.F., **P.J. Mahoney**, and B. Patterson. 2015. Spatiotemporal variation in

selection of roads influences mortality risk for canids in an unprotected landscape. *Oikos* 124:1664-1673.

Mahoney, P.J., K.H. Beard, A.M. Durso, *et al*. 2014. Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. *Diversity and Distribution* 21:64-74.

Benson, J.F., B. Patterson, and **P.J. Mahoney**. 2014. A protected area influences genotype-specific survival and the structure of a *Canis* hybrid zone. *Ecology* 95:254-264.

Mahoney, P.J., K.D. Meyer, G.M. Zimmerman, and C.E. Cattau. 2010. An aquatic Bal-Chatri for trapping Snail Kites (*Rostrhamus sociabilis*). *Southeastern Naturalist* 9:721-730.

PUBLICATIONS IN PREPARATION

* *First authorship may change depending on time constraints*

Mahoney, P.J., J.K. Young, D. Stoner, K. Hersey, and L. McFarlane. *In prep*. Assessing aerial removal risk in western coyotes (*Canis latrans*) and the implications for mule deer (*Odocoileus hemionus*) population dynamics using spatially-explicit Bayesian hierarchical models. *Journal of Applied Ecology*.

Mahoney, P.J. and J.K. Young. *In prep*. Cats and Dogs: behavioral responses of a subordinate canid to carrion subsidies associated with simulated large felid prey caches. *Animal Behaviour.*

Mahoney, P.J., D. Stoner, L. McFarlane, and J.K. Young. *In prep*. Functional responses in cougar (*Puma concolor*) space use in relation to human hunting pressure.

Mahoney, P.J., D. Stoner, L. McFarlane, and J.K. Young. *In prep*. Catch a lion by the tail: the dynamics of concurrent space use in coyotes (*Canis latrans*) and mountain lions (*Puma concolor*). *Ecology*.

***Mahoney, P.J.**, D. Schaible, K. Hersey, and J.K. Young. *In prep*. Elk (*Cervus elaphus*) movement ecology in southern Utah: assessing the relative contributions of human and environmental factors on elk resource utilization using a combination of step-selection and hidden Markov models.

Breck, S.W., **P.J. Mahoney**, and J.K. Young. *In prep*. Dynamic behavioral responses in coyotes (*Canis latrans*) to novel objects along an urban-rural gradient.

Kleuver, B, **P.J. Mahoney**, S.J. Dempsey, and E.M. Gese. *In prep*. The influence of

dynamic water sources on coyote (*Canis latrans*) space use in desert environments.

OTHER PUBLICATIONS

Murray, D.L., T.D. Steury, and **P.J. Mahoney**. 2012. Viability of the reintroduced red wolf population in North Carolina. Final Report, U.S. Fish and Wildlife Service.

Mahoney, P.J., T.D. Steury, and D. Murray. 2011. The role of behavior in predicting red wolf (*Canis rufus*) persistence potential: an individual-based modeling approach. Auburn University, Master's Thesis.

Mahoney, P.J., T.D. Steury, and D. Murray. 2011. Predictive accuracy in population viability models: the red wolf as a model system. Auburn University, Master's Thesis.

A plate in: Demski, L.S. 2003. In the Fish's Mind's Eye: The Visual Pallium of Teleosts. In: Sensory Processing in Aquatic Environments (Collin, S.P. and Marshall, N.J., eds.), pp. 404 – 419, Springer- Verlag.

Mahoney, P. 2001. The cytoarchitecture of the telencephalon of a cichlid fish: *Cichlasoma cyanoguttatum*. New College of Florida, Undergraduate Thesis.

TEACHING EXPERIENCE

Workshop Instructor

- "Assessing resource utilization in program R: from machine learning to multi-level Bayesian GLMs", Peter Mahoney and Michel Kohl, USU Workshop, Spring 2016
- "Known-fate modeling", Peter Mahoney and John Benson, TWS - Colorado Chapter, February 2016
- "Intro to Rstan: the basics of Bayesian programming in R", Peter Mahoney, USU Ecolunch, December 2015
- "Known-fate modeling", Peter Mahoney and John Benson, National TWS, October 2015
- "AIC model selection and multimodal inference", Peter Mahoney, USU Workshop, Spring 2013

Guest Lecturer / Teaching Assistant
Sept 2011 – Present
Utah State University

- "Evaluating avian movement and home range utilization", *USU Guest Lecturer* for Dr. Frank Howe, Spring 2016.

- "Program MARK", *Teaching Assistant* for Dr. Mary Conner, Spring 2015
- "Species diversity and abundance", *USU Guest Lecturer* for Dr. Dustin Ranglack, Spring 2015
- "Dynamics of predator-prey systems", *SUU Guest Lecturer* for Dr. Nicki Frey, Spring 2014
- "Population viability analyses", *USU Guest Lecturer* for Dr. Karen Beard, Spring 2013
- "Base R Programming" for Utah Division of Wildlife Biologists, *Teaching Assistant* for Dr. Tom Edwards, Spring 2012
- "Computer programming and database management for biologists", *Teaching Assistant* for Dr. Ethan White, Spring 2012

Graduate Teaching Assistant
Jan. 2009 – May 2011
Auburn University
- Taught laboratory extensions for Principles of Wildlife Ecology and Wildlife Management II.
- Guest lecturer:
  "Red Wolf Recovery: the past and future"
  "Historical reintroductions in the United States"

Secondary Education Science

Jan. 2003 – June 2005	Hardee Senior High School	Wauchula, FL
Aug. 2001 – Aug. 2002	Booker Senior High School	Sarasota, FL

PROFESSIONAL FIELD EXPERIENCE

Graduate Research Assistant
Aug. 2011 – Present
Utah State University, Logan, UT
- Managed field logistics and data collection for all cougar research in the state of Utah.
- Assist state houndsman with cougar captures via horseback.
- Conduct non-invasive surveys for cougars and coyotes throughout Monroe Mountain, Fishlake National Forest, Utah.
- Conduct small mammal (Sherman trap grids) and lagomorph (spotlight) surveys in order to estimate alternative prey abundance.
- Capture coyotes using Victor 3 soft-catch leg hold traps and cable restraints.
- Monitor study animals year-round using telemetry at elevations between 4,500 – 11,000 feet.
- Assist with deer and elk helicopter captures (200+), which included VIT tagging, radio- collaring, and determining body condition through ultrasounds of rump and

loin fat.

Field Biologist
May 2011 – Aug. 2011
US Forest Service, Lander, WY
- Managed volunteers for a statewide ferruginous hawk project.
- Assisted with study design.
- Surveyed small mammal abundance near hawk nesting sites.
- Monitored hawk nesting success.

Eastern Wolf Den Crew Technician
May 2010 – June 2010
Trent University, Ontario, Canada
- Volunteered the two prior seasons for a total of three seasons.
- Aided and advised a Trent University student with field logistics.
- Captured wolf pups and assisted veterinarians in implanting VHF transmitters.
- Monitored transmittered wolves from the ground and air.
- Recovered mortalities and determined cause of death.

Avian Field Technician
March 2006 – Aug. 2008
Avian Research and Conserv. Inst. (ARCI), Gainesville, FL
- Managed field logistics for a large number of avian research projections, including several with an emphasis on endangered and threatened species.
- Assisted in project development, implementation, and data organization.
- Coordinated various field activities with project leaders and non-employee personnel.
- Supervised volunteers and technicians.
- Vehicle maintenance (all types).

PRESENTATIONS

Benson J.F, **P.J. Mahoney**, J.A. Sikich, L.E.K. Serieys, J.P. Pollinger, R.K. Wayne, H.B. Ernest, and S.P.D. Riley. Modeling population viability and inbreeding dynamics of a small, isolated mountain lion population adjacent to Los Angeles. The Wildlife Society, *February 2016*, Colorado Springs, CO.

Mahoney, P.J., J.K. Young, and D.C. Stoner. Evaluating coyote removal risk: Spatial implications for mule deer. The Wildlife Society, *October 2015*, Winnipeg, Manitoba, Canada. Poster.

Benson J.F, **P.J. Mahoney**, J.A. Sikich, L.E.K. Serieys, J.P. Pollinger, R.K. Wayne, H.B. Ernest, and S.P.D. Riley. Modeling population viability and inbreeding dynamics of a small, isolated mountain lion population adjacent to Los Angeles. The Wildlife Society, *October 2015*, Winnipeg, Manitoba, Canada.

Benson J.F, **P.J. Mahoney**, J.A. Sikich, L.E.K. Serieys, J.P. Pollinger, R.K. Wayne, H.B. Ernest, and S.P.D. Riley. Modeling population viability and inbreeding dynamics of a small, isolated mountain lion population adjacent to Los Angeles. International Urban Wildlife Conference, *May 2015*, Chicago, Illinois, USA.

Beard, K.H., R. Tingley, **P.J. Mahoney**, A.M. Durso, A.G. Tallian, and A. Morán-Ordóñez. Extinction and invasion risk are not two sides of the same coin, at least for reptiles. International Congress for Conservation Biology, *Aug 2015*, Montpellier, France.

Beard, K.H., **P.J. Mahoney**, A.G. Taillan, A.L.Long, A.M. Durso, R.J. Kindermann, N.E. Nolan, D. Kinka, and H.E. Mohn. Getting to the bottom of reptile establishment success. North American Congress for Conservation Biology, *July 2014*, Missoula, Montana, USA.

Mahoney, P., K.H. Beard, A.M. Durso, A. G. Taillian, A. L. Long, R. J. Kindermann, N. E. Nolan, D. Kinka, and H. E. Mohn. Introduction effort, climate matching, and species traits as predictors of global establishment success in non-native reptiles. Joint Meeting of Ichthyologists & Herpetologists, *August 2014*, Chattanooga, Tennessee, USA.

Mahoney, P.J., J.K. Young, and J.A. Shivik. Program Cluster: Identifying Predation Events Through Clustered GPS Data. Eleventh Mountain Lion Workshop, *12 – 15 May 2014*, Cedar City, Utah, USA.

Young, J.K., **P.J. Mahoney**, and J.A. Shivik. Cougar space use on a landscape with high levels of anthropogenic disturbance in southcentral Utah. Eleventh Mountain Lion Workshop, *12 – 15 May 2014*, Cedar City, Utah, USA.

Mahoney, P.J. and J.K. Young. Cougar predation of coyotes: Implications for mule management. Gordon Research Conference on Predator-prey Interactions, *5 – 10 January 2014*, Ventura, California, USA. Poster.

Mahoney, P.J., J.K. Young, D.C. Stoner, J.A. Shivik, S.M.C. Cavalcanti, and E.M. Gese. Find that Cache: Identifying Predation Events Through Clustered GPS Data. The Wildlife Society, Utah Chapter, 20 March – 22 March 2013, Bryce City, Utah, USA. **(See Awards)**

Mahoney, P.J., T.D. Steury, and D. Murray. A re-assessment of Red Wolf (*Canis*

rufus) viability using stage-structured, stochastic population models. Carnivores, 15 – 18 November 2009, Denver, Colorado, USA.

GRANTS

USU Ecology Center Student Award, $4,000	2012
Drummond Company Fellowship, $1,500	2010
Graduate Research Fellowship, University of Queensland, $22,000 per year	2003
Sarasota County, Florida Grant, $5,000 to measure the productivity of artificial reefs in Sarasota Bay	1999

AWARDS

Best Student Paper for The Wildlife Society, Utah Chapter	2013
Auburn University Outstanding Master's Student of the Year	2010
School of Forestry and Wildlife Science Outstanding Master's Student of the Year	2010
Alumni representative on the Pritzker Marine Laboratory Advisory Committee	2001- 2002

PROFESSIONAL SERVICE

Reviewer:
- Animal Behaviour
- Biological Conservation
- Ecosphere
- Global Ecology and Biogeography
- Journal of Herpetology
- Society for Conservation Biology

Wild Felid Association - Utah Student Representative, 2013-2015
Pritzker Marine Alumni Representative, New College of Florida, 2002-2003
Natural Sciences Student Representative, New College of Florida, 1998-1999